

MADROÑO
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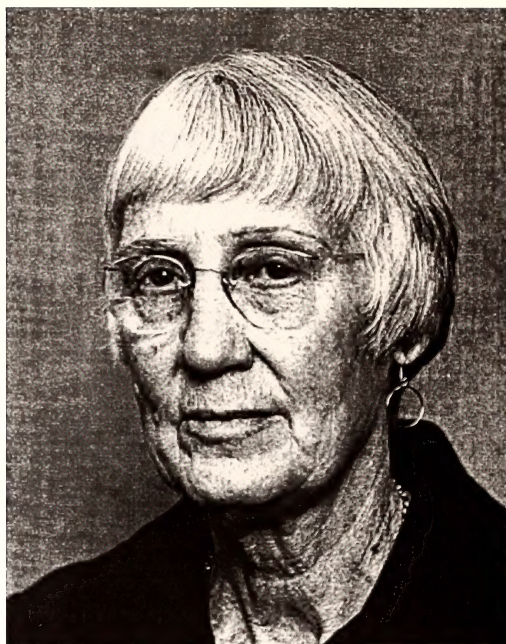
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DEDICATION¹

Lauramay Tinsley Dempster's life spanned most of the 20th century (1907–1997) and her botanical career spanned more than 6 decades and her scientific field work six continents. At her desk at the University and Jepson Herbaria is 1997 research-and-writing in progress; in the herbarium library down the hall is Lauramay Tinsley's 1927 thesis.

Most of her professional and personal life was in association with the University of California at Berkeley, where she came at sixteen as a freshman. At the University, she received her bachelor's degree in 1925 and a master's degree (with Willis Linn Jepson) in 1927. She was Jepson's research assistant for many years and a Research Associate there for the last three decades. Her husband Everett Ross Dempster received his Ph.D. and was a faculty member and department chair.

As Jepson's assistant (which lasted essentially until his death in 1946), Lauramay devoted her research, writing, and drawing talents, her laborious typing and proof-reading, to the completion of Jepson's *Flora of California*, and his other pursuits. As she herself noted, he was chary in bestowing credit, but the worth of his projects to her transcended his self-centeredness.

¹ We would like to thank Richard G. Beidleman for compiling the information and Tony Morosco for composing the photographs (which are from the Jepson and UC Herbaria archives).

It was Rimo Bacigalupi, the first curator of the Jepson Herbarium, who suggested that Lauramay, now free of obligations to Jepson, initiate research on *Galium* (Rubiaceae) and its relatives. That began her innumerable field trips throughout California, often by herself, but also with family and colleagues, especially G. Ledyard Stebbins. Her field work extended beyond California—and beyond *Galium*—to Alaska, Mexico, South America, the Galapagos, Europe, Australia, Africa, and Antarctica.

She published a number of scientific papers, primarily on *Galium*, as sole author and in collaboration; she was senior author when she wrote with Stebbins. In 1979, she was the author of Volume 4 Part 2 (Rubiaceae) of Jepson's *Flora*. When the revision of *The Jepson Manual* appeared in 1993, Lauramay had authored or co-authored not only the section on her specialty, the Rubiaceae, but also five other major treatments. One-fourth of the California *Galium* species received their specific epithets from Lauramay, either alone or as senior author. And, in her nineties, she completed her treatment of *Galium* for the *Flora of North America*.

Her research was supported for many years by grants from the National Science Foundation. In 1965, she appeared in *American Men of Science*, when it was still called *American Men*. In her 'spare' time, she found time to be active in the Society of Women Geographers, University Women's Club, and American Society of Plant Taxonomists, to play the oboe, to paint a tropical forest panoramic mural across the entire south front room wall of the family home in Orinda and a wildflower mural in the bedroom.

Lauramay always regretted that she had not published her thesis on *Lepidium*. Most recently, she regretted that it became physically so difficult to get from the campus parking lot across to her haunts in the herbarium, to continue research and writing . . . and chatting with her much younger colleagues.

But all of us who have enjoyed being her colleagues feel that she should have had no regrets. Hers was indeed a long, full, and immeasurably salutary life. And she gave us science, friendship, advice, and inspiration. So, we dedicate Madroño volume 44 to Lauramay Tinsley Dempster².

² A more complete biography will appear in an obituary in volume 45.

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SYNOPTICAL KEYS TO GENERA OF CALIFORNIAN COMPOSITES

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ABSTRACT

Synoptical keys are sometimes preferred to artificial keys. In the synoptical keys provided here, the 207 genera of composites recognized in *The Jepson Manual* represent 2 of the 3 subfamilies and 13 of the 16 tribes used in a classification system differing only slightly from that proposed by Bremer in 1994. Of the 207 genera treated in *The Jepson Manual*, Heliantheae (incl. Helenieae), as circumscribed here, includes 78 (distributed among 17 subtribes) and Astereae and Lactuceae have 33 each. The other ten tribes are represented in *The Jepson Manual* by 1 to 14 genera each.

David Keil (in Hickman 1993) provided excellent, wonderfully workable, well-received artificial keys for identification of genera of composites as treated in *The Jepson Manual* (*JepsMan*). Some plant identifiers readily assimilate characteristics of artificial groupings of taxa and they readily accept artificial keys such as those written by Keil. Other plant identifiers have difficulty assimilating artificial groups but they do readily recognize individual plants as members of certain natural groups, even if they do not recognize the particular species or genus to which an individual plant belongs. Upon finding an artichoke in flower, for example, they may not recognize or "know" the genus to which the plant belongs but they do recognize that it belongs in the tribe with thistles, Cardueae. Some such users of *JepsMan* expressed interest in having synoptical keys to genera organized into natural groups (i.e., into tribes and subtribes). The following notes, diagnoses, and keys were prepared in response to that expressed interest.

Notes. In the classification on which the following treatment is based, 3 subfamilies and 16 tribes are recognized. Representatives of 2 subfamilies and 13 tribes are found among the 207 genera of composites treated in *JepsMan*. Barnadesioideae and its only tribe, Barnadesieae, and two tribes from Cichorioideae (Vernonieae and Liabeae) are not represented in *JepsMan*.

Tribal circumscriptions adopted here match those adopted by Bremer (1994) except that Helenieae and Heliantheae sensu Karis and Ryding (1994a, b) are treated as one tribe, Heliantheae. Tribal and subtribal circumscriptions and classification for Heliantheae used here are sensu H. Robinson (1981). Tribal circumscriptions and classifications for

Gnaphalieae, Inuleae, and Plucheeae are sensu Anderberg (1994a, b, c).

In writing tribal diagnoses, I have tried to balance economy of print with sufficiency of detail and parallel construction. In large measure, the tribal diagnoses are derived from those found in *Manual of the Flowering Plants of California* by W. L. Jepson (1925) and are intended to account only for plants found growing without cultivation within California.

Generic characteristics used in constructing keys have, for the most part, been taken directly from the descriptions in *JepsMan*. So far as practicable, generic characteristics have been verified in specimens in nature and in herbaria, especially in JEPS and in UC, and in accounts (floras, monographs, and revisions) by other authors. Principal publications consulted were Bentham (1873), Bremer (1994), Ferris (1960), Hickman (1993), Jepson (1925), and Robinson (1981). Also, sequence of characteristics in each lead in my keys is usually that commonly used in descriptions. The first trait mentioned in each lead is not necessarily the "best" or "most reliable" or "most easily assessed."

Terms. Composites share some morphological traits not found in other families of plants, much as do grasses, legumes, orchids, et al. Some of the terms (and spellings) I use in characterizations of composites differ from those used in *JepsMan* and I use some terms in somewhat different senses than they are used in *JepsMan*. The differences are unfortunate. A reviewer suggested that I continue using terms and usages as found in *JepsMan*. I considered and rejected that choice. My usages are briefly reviewed below and are amplified upon where appropriate within the diagnoses and keys.

Inflorescences of composites are called **heads** or capitula. Heads typically comprise multiple florets (small flowers) of one or more kinds borne on a common **receptacle**. The florets are collectively subtended by an **involucre** of bracts (involucral bracts), here called **phyllaries**. Individual florets may be individually subtended by receptacular bracts, here called **paleae** (sing., palea). In *JepsMan*, receptacular paleae are called "chaff scales." In some other floras, scales of a pappus may be called paleae.

Heads are often characteristically arranged on composites, much as individual flowers are on other kinds of plants. Such arrays of heads are collectively referred to as **capitulescences**. Different forms of capitulescences are referred to by using terms derived from terms for inflorescences: corymbiform, racemiform, spiciform, etc.

In plants with **liguliflorous** heads (e.g., dandelions), all florets in each head are bisexual, fertile, and zygomorphic; all florets in such heads are said to be **ligulate florets**. In **radiate** heads (e.g., daisies), the peripheral florets (**ray florets**), in one or more series, have corollas with zygomorphic limbs and the inner florets (**disc florets**) have acti-

nomorphic corollas. Ray florets may be pistillate (i.e., styliferous and fertile), styliferous and sterile, or neuter; disc florets may be bisexual (producing functional pollen and ovules) or functionally staminate (producing functional pollen but without functional ovules). In **discoid** heads (e.g., *ageratum*s), all florets are bisexual and fertile and have actinomorphic corollas. Technically, disc florets are found only in radiate heads. Traditionally (and here), all florets in a discoid head are called disc florets; they correspond morphologically to the true disc florets of radiate heads. In **disciform** heads (e.g., most everlastings), the peripheral florets (in one or more series) are pistillate and usually have relatively slender corollas with minute lobes (sometimes the peripheral florets lack corollas); the inner florets may be bisexual or functionally staminate and have actinomorphic corollas. In **radiant** heads (e.g., cornflowers), the peripheral florets have much enlarged, actinomorphic to somewhat zygomorphic corollas and may be bisexual, pistillate, or neuter; the inner florets are bisexual and have actinomorphic corollas.

Heads with all florets of one sexual form are called **homogamous** (discoid, liguliflorous, and some radiant heads) and those with florets of two or more sexual forms are called **heterogamous** (radiate, disciform, and most radiant heads).

Despite folklore to the contrary, composites do not always have yellow corollas. Particular corolla colors *are* characteristic of some groups of genera. As used here, **cyanic** includes true blues, mauves, pinks, purples, reds, etc.

In descriptions of corollas of composites, the terms tube, throat, and limb have been variously used. Here, for actinomorphic corollas of bisexual and functionally staminate florets, **tube** refers to the part of the corolla proximal to the insertion of the staminal filaments and **limb** refers to the part that is distal to insertion of the filaments. The limb of the corolla of a disc floret comprises a proximal **throat** and (3–)5 distal **lobes**. As treated here, the distinction between tubes and throats of corollas of disc florets is determined by insertion of filaments, not by external morphology.

The relatively flat, \pm linear, tongue-shaped or strap-shaped, zygomorphic portion of a ligulate corolla is here called a **ligule**. A ligule terminates in 5 teeth or lobes. The similar, relatively flat, zygomorphic portion of a corolla of a ray floret is here called a **lamina**. A lamina terminates in 0–3(–4) teeth or lobes. In *JepsMan*, the term *ligule* is used for corollas of both ray florets and ligulate florets. Bilabiate corollas are characteristic of some members of Mutisieae and are seldom found in members of other tribes.

Stamens of composites characteristically are synantherous; the anthers are connate. The individual pollen sacs of each anther may extend below the insertion of the filament (calcarate anthers) or not (ecalcarate anthers). The pollen sacs characteristically bear tails (the

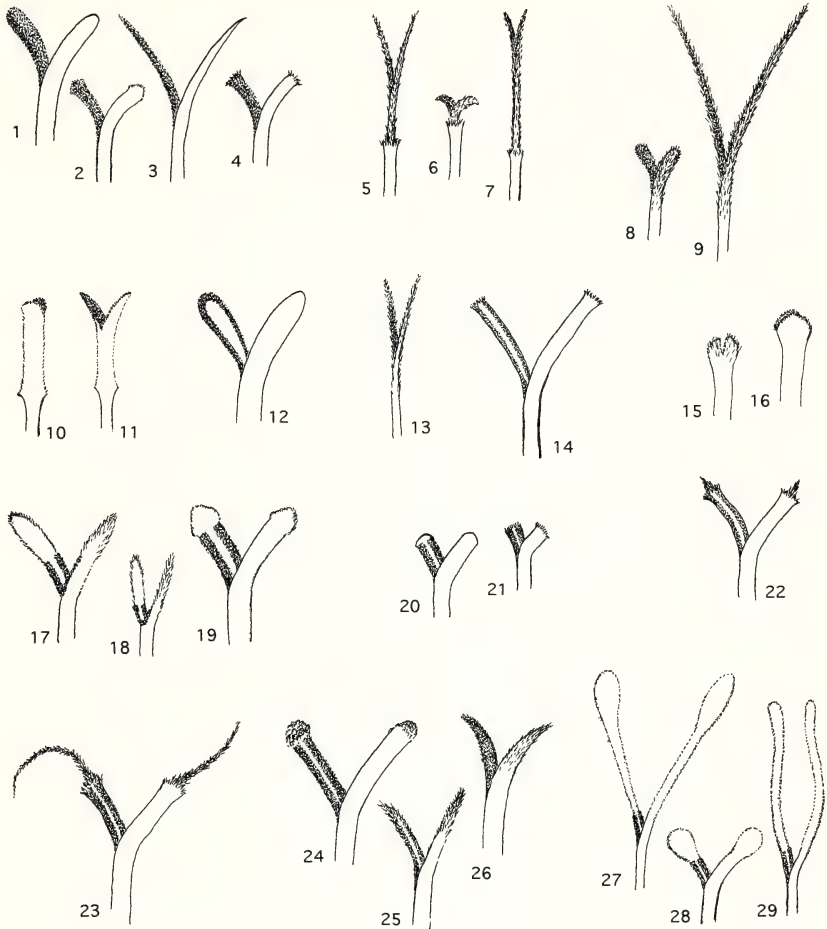
anthers are caudate) in members of the cichorioid tribes (Arctoteae, Cardueae, Lactuceae, Liabeae, Mutisieae, and Vernonieae) and in some asteroid tribes (Inuleae, Plucheeae, Gnaphalieae, and Calenduleae). Anthers of other asteroid composites (Anthemideae, Astereae, Eupatorieae, Heliantheae, and Senecioneae) usually lack tails (the anthers are ecaudate).

Style characteristics such as lengths and shapes of branches, distribution of stigmatic papillae, and shape and vestiture of stylar appendages are uniform across some tribes. Style characteristics are usually determined from bisexual, rarely from functionally staminate, florets (cf. Figs. 1–29).

Fruits of composites have been called “achenes” because they resemble true achenes. Achenes are dry, hard, single-seeded fruits derived from unicarpellate ovaries. Ovaries of composites are bicarpellate. Fruits derived from ovaries of composites are called **cypselae** (sing., cypsel). Shapes and ornamentations of cypselae have been used in distinguishing among genera. In some genera, the cypselae are characteristically \pm lenticular in cross section. Such cypselae are said to be **compressed** or laterally flattened if the longer axis of the cross section is \pm parallel to a radius of the head (e.g., *Helianthus* spp.). Cypselae are said to be **obcompressed** or dorsiventrally flattened if the shorter axis of the cross section is \pm parallel to a radius of the head (e.g., *Coreopsis* spp.).

Distal on the ovary of a composite, just proximal to the corolla, a **pappus** is usually present. Pappus may be homologous with the calyx of other flowers or it may be a novel structure. Pappi show a great range of diversity and are often diagnostic for recognition of genera of composites. The various forms of individual pappus components intergrade. Here, the following arbitrary distinctions are made: Pappus **bristles** and **awns** have \pm circular or polygonal cross sections with the length of the longer diameter of the cross section no more than 3 times that of the shorter diameter. Pappus elements with “flatter” cross sections (i.e., length of longer diameter more than 3 times that of the shorter diameter) are called **scales**, regardless of relative overall length of the pappus element. As used here, “subulate scale” means much the same as “flattened bristle,” as used in *JepsMan* and some other floras. Pliable to stiff bristles with diameters less than ca. 50 μm are called **fine bristles**; pliable to stiff bristles with diameters greater than ca. 50 μm are called **coarse bristles**. Rigid elements with \pm circular or polygonal cross sections greater than 100 μm in diameter are called **awns**. Bristles, awns, and scales may be smooth or, variously, finely to coarsely barbed or plumose. Each scale of a pappus may terminate in one or more bristle-like or awn-like appendages; such scales are said to be **aristate**; the aristae may be smooth, \pm barbellate, or plumose.

Caveat. The following keys are intended for use with Californian specimens of genera of composites as circumscribed in *JepsMan*.



FIGS. 1-29. Style branches from bisexual and functionally staminate florets representative of forms found in some tribes of Compositae. 1-4. Mutisieae. 5-7. Cardueae. 8-9. Lactuceae. 10-11. Arctoteae. 12. Inuleae. 13. Plucheeae. 14. Gnaphalieae, some Heliantheae, Senecioneae. 15-16. Calenduleae. 17-19. Astereae. 20-21. Anthemideae. 22. Senecioneae, some Heliantheae. 23. Heliantheae, some Senecioneae. 24-26. Heliantheae. 27-29. Eupatorieae.

For these keys, I have accepted generic circumscriptions as given. I assume no responsibilities for cavalier users of these keys who may rashly attempt to ply them with other taxonomies or with specimens from elsewhere.

Some couplets here are essentially statements of contrasting probabilities (e.g., corollas yellow in most spp. vs. corollas white in most spp.) rather than statements of contrasting absolutes (e.g., corollas yellow in all spp. vs. corollas white in all spp.). My failure to write

couplets based solely on absolutes may inform users about my ability to write keys. Or, my failure may inform users about circumscriptions of genera, subtribes, and tribes of composites.

KEY TO TRIBES

1. Sap usually milky; heads liguliflorous, florets all bisexual and corollas all zygomorphic, all ligulate (i.e., corolla limbs laminar, \pm linear to flabellate, and 5-lobed or 5-toothed)—styles mostly as in Figs. 8–9. II.C. Lactuceae
- 1' Sap rarely milky; heads not liguliflorous, florets bisexual, unisexual, or neuter and corollas zygomorphic or actinomorphic, none truly ligulate (i.e., corolla limbs in bisexual florets not both laminar and distally 5-lobed or 5-toothed).
 2. Corollas all zygomorphic, all bilabiate—styles mostly as in Figs. 1–4. II.A. Mutisieae p.p.
 - 2' Corollas not all zygomorphic, not all bilabiate, some or all corollas \pm actinomorphic.
 3. Cypselae stalked-glandular—styles of inner, functionally staminate florets undivided. II.A. Mutisieae p.p. (*Adenocaulon*)
 - 3' Cypselae not stalked-glandular.
 4. Actinomorphic corollas deeply cleft, lobes 5, mostly linear, length more than 3 times width in most spp.; anthers calcarate (filament insertion distal to bases of anther sacs) and tailed in most spp.; styles distally dilated or thickened or with a ring of hairs proximal to the branches in many spp., stigmatic surface continuous on adaxial face of each branch (stigmatic papillae not in 2 distinct or contiguous lines).
 5. Florets 1 in each head, the primary heads collected in second-order heads.
 6. Shrubs, mostly 4–7 dm high; leaves usually prickly-dentate, not lobed; cypselae glabrous or glabrate—style branches minute, not figured. II.A. Mutisieae p.p. (*Hecastoleis*)
 - 6' Herbs, thistle-like, mostly 1–2 m high; leaves prickly-margined, pinnately lobed; cypselae villous—styles as in Figs. 5–6. II.B. Cardueae p.p. (*Echinops*)
 - 5' Florets 3–100+ in each head, the heads not collected in second-order heads.
 7. Heads radiate (peripheral florets pistillate or neuter, corollas zygomorphic, the limb of each laminar, 3–4-toothed); pappi none or of ovate scales—styles mostly as in Figs. 10–11. II.F. Arctoteae
 - 7' Heads discoid, disciform, or radiant, not radiate; pappi of bristles (often plumose), setiform scales, or none—styles mostly as in Figs. 5–7. II.B. Cardueae p.p.
 - 4' Actinomorphic corollas not deeply cleft, lobes (3–)5, \pm deltate, length less than 3 times width in most spp. (pistillate florets may lack corollas in some spp.); anthers ecalcarate in most spp., not tailed in most spp. (but see couplet 8); styles not distally thickened nor with a ring of hairs proximal to the branches, stigmatic surfaces in 2 separate lines on each branch in most spp., in 2 contiguous lines in some spp., continuous in very few spp.
 8. Anthers distinctly tailed in most spp. [Among our plants with tailed anthers, some are woolly annuals 1–3(–10) cm high with involucre 1–3 mm high and corollas 0.5–1 mm long. III.C. Gnaphalieae p.p.]

9. Heads radiate (peripheral florets pistillate or neuter, their corollas zygomorphic with laminar, 2–3-toothed limbs).
10. Cypselae usually tuberculate, reticulate-ridged, or winged, rarely smooth, not 5-ribbed; pappi none—styles mostly as in Figs. 15–16. III.D. Calenduleae
- 10' Cypselae \pm 5-ribbed, not ridged, tuberculate, or winged; pappi of bristles or of scales and bristles—styles mostly as in Fig. 12. III.A. Inuleae
- 9' Heads discoid or disciform, all florets with actinomorphic corollas, or corollas wanting.
11. Phyllaries 12–30+ in 3–5+ series, herbaceous, not strongly scarious or broadly scarious-margined—styles mostly as in Fig. 13. III.B. Plucheeae
- 11' Phyllaries none, or 3–10 in 1–2 series, or, if 12–30+ in 3–5+ series, then strongly scarious or broadly scarious-margined—styles mostly as in Fig. 14. III.C. Gnaphalieae
- 8' Anthers not tailed (sagittate in some spp.). [Rarely diminutive woolly annuals with very small heads and corollas.]
12. Heads discoid; corollas white or pinkish to purplish, never yellow; style appendages terete to clavate, 2–3+ times longer than the stigmatic lines in most spp., shorter and \pm flattened in few spp.—see Figs. 27–29. III.I. Eupatorieae
- 12' Heads radiate, discoid, disciform, or radiant; corollas of the disc florets yellow, orange, or brown in most spp., white or cyanic in very few spp.; style appendages less than 2 times as long as stigmatic lines in most spp., longer in very few spp.
13. Phyllaries in 3–5 series and unequal in most spp., margins scarious in most spp.; pappi none or coroniform—styles mostly as in Figs. 20–21; cypselae not papillate. III.F. Anthemideae
- 13' Phyllaries in 1–2 series and \pm equal or in 3–5+ series and unequal, margins not scarious in most spp.; pappi none or variously of scales and/or bristles and/or awns, coroniform in very few spp.
14. Leaves alternate; phyllaries in 1–2 series and subequal in most spp., sometimes coherent, actually free to base or nearly so, involucre proper subtended by a calyculus of bractlets in some spp. (phyllaries in 3+ series and graduated in *Lepidospartum*); receptacles epaleate; cypselae \pm columnar to fusiform or obovoid, not strongly compressed or obcompressed, in most spp.; pappi of 30–100+ fine bristles (never plumose) in most spp. (subulate scales in some *Tetradymia* spp.), pappi none in very few spp.—styles mostly as in Fig. 22, sometimes as in Fig. 14 or 23. III.G. Senecioneae
- 14' Leaves opposite or alternate; phyllaries subequal in 1–2 series or graduated in 3–5+ series, \pm connate in some spp., involucre subtended by a calyculus in few spp. (cf. Heliantheae–Coreopsidinae and Heliantheae–Pectidinae); receptacles pa-

leate or epaleate; cypselae various, often compressed or obcompressed; pappi none or of scales and/or bristles and/or awns.

15. Leaves all alternate in most spp., basal in some spp.; phyllaries graduated in 3–5+ series in most spp., subequal in very few spp., mostly linear to oblanceolate; receptacles epaleate (except *Eastwoodia*, *Rigiopappus*, and some *Baccharis* spp.); laminae of ray corollas becoming coiled like watch springs or butterfly probosci in most spp.; anthers connate; pappi usually of bristles, seldom of scales—style-branch appendages glabrous adaxially, mostly as in Figs. 17–19. . . .

..... III.E. Astereae

- 15' Leaves opposite (at least proximally) in most spp., alternate in some spp., basal in some spp.; phyllaries subequal in 1–3 series (then linear to lanceolate) or graduated in 3–5+ series (then lanceolate to ovate or broader); receptacles paleate or epaleate; laminae of ray corollas very rarely coiled; anthers connate or free; pappi usually of scales or awns, seldom of bristles—style-branch appendages usually loosely papillose or hairy adaxially, mostly as in Figs. 23–26, sometimes as in Figs. 14, 21, 22. . . .

..... III.H. Heliantheae

I.A. Barnadesieae.

No members of the tribe were treated in *JepsMan*.

II.A. Mutisieae.

Shrubs, herbs. Leaves basal and/or cauline; alternate. Phyllaries in 1–3 series, unequal. Receptacles epaleate—hairy or glabrous. Heads radiate, disciform, or discoid. Corollas zygomorphic (often 2-lipped) or actinomorphic, usually with long lobes, sometimes with short lobes—yellow/orange, cyanic, or white. Anthers calcarate, tailed. Style branches abaxially hispidulous, stigmatic areas continuous, apices acute to rounded or truncate (Figs. 1–4). Cypselae columnar, fusiform, or clavate—often ribbed. Pappi of bristles or coriiform or none.

Key to genera as treated in *JepsMan*

1. Scapiform herbs; leaves mostly in basal rosettes, the blades white-tomentose abaxially; cypselae stalked-glandular. *Adenocaulon*
- 1' Non-scapiform herbs or shrubs; leaves cauline, the blades not white-tomentose abaxially; cypselae not stalked-glandular.
 2. Florets 1 in each head (heads grouped into second-order heads); corollas actinomorphic. *Hecastocleis*
 - 2' Florets 10–20+ in each head; corollas bilabiate.

3. Herbs; corollas pink to white. *Acourtia*
 3' Shrubs; corollas yellow. *Trixis*

II.B. Cardueae.

Herbs, sometimes coarse, to 2+ m tall. Leaves basal and/or cauline; alternate—often pinnately divided, often prickly. Phyllaries in 3–5+ series, unequal—often prickly or spine-tipped. Receptacles epaleate, often hairy or setose. Heads discoid, disciform, or radiant. Corollas mostly actinomorphic with long lobes, rarely weakly zygomorphic—yellow, cyanic, or white. Anthers calcarate, tailed. Styles dilated or with ring of hairs proximal to branches, branches short or linear, stigmatic areas continuous (Figs. 5–7). Cypselae mostly obovoid, often compressed—insertion often lateral. Pappi of bristles or subulate scales, the elements often plumose.

Key to genera treated in *JepsMan*

1. Florets 1 per head, heads grouped into globose, second-order heads. *Echinops*
- 1' Florets 3–250+ per head, heads not in second-order heads.
 2. Leaves not thistle-like, the margins not prickly (phyllaries may have prickly margins).
 3. Carpodia and insertion scars of cypselae \pm lateral at bases of cypselae.
 4. Heads discoid, disciform, or radiant; peripheral florets often neuter or pistillate and sterile; pappi none or of persistent, nonplumose bristles or scales. *Centaurea*
 - 4' Heads discoid; all florets fertile; pappus bristles not persistent, usually \pm plumose. *Acroptilon*
 3. Carpodia \pm central at bases of cypselae.
 5. Annuals; heads disciform; peripheral florets sterile. . . . *Crupina*
 - 5' Biennials and perennials; heads discoid; all florets fertile.
 6. Phyllary tips usually attenuate, uncinat; pappus bristles not connate, not plumose. *Arctium*
 - 6' Phyllary tips not attenuate, rarely uncinat; pappus bristles basally connate, distally plumose.
 7. Largest leaves 5–15 cm long; involucre 5–12 mm diam.; florets 10–20 per head. *Saussurea*
 - 7' Largest leaves 60–150+ cm long; involucre 35–100+ mm diam.; florets 100–250+ per head. . . . *Cynara* p.p.
 - 2' Leaves thistle-like, the margins prickly.
 8. Stems notably winged, the wing margins prickly.
 9. Receptacles setose-bristly, not deeply pitted; pappus bristles free. *Carduus*
 - 9' Receptacles deeply pitted, not bristly; pappus bristles basally connate. *Onopordum*
 - 8' Stems rarely winged (sometimes narrowly winged in *Cirsium* spp.).
 10. Leaves variegated with white veins or mottlings; stamen filaments connate. *Silybum*
 - 10' Leaves not variegated; stamen filaments free.
 11. Corollas white or purplish to red; carpodia and insertion scars \pm at centers of bases of cypselae; pappi of basally connate, plumose bristles.

- 12. Largest leaves 20–50(–110) cm long; involucre 10–50 mm diam.; phyllaries ovate to linear; receptacles not becoming very fleshy. *Cirsium*
- 12' Largest leaves 60–150+ cm long; involucre 35–100+ mm diam.; phyllaries ovate to elliptic; receptacles becoming fleshy. *Cynara* p.p.
- 11' Corollas yellow to orange; carpopodia displaced adaxially (toward center of receptacle) at bases of cypselae; pappi none or of free, nonplumose bristles or scales.
- 13. Heads discoid, all florets fertile; receptacles paleate; cypselae \pm 4-angled. *Carthamus*
- 13' Heads disciform, peripheral florets sterile; receptacles setose-bristly; cypselae 20-ribbed. *Cnicus*

II.C. **Lactuceae.**

Shrubs, herbs—sap milky white. Leaves basal and/or cauline; usually alternate, rarely opposite—often pinnately divided. Phyllaries in 2–5+ series, subequal to unequal—sometimes subtended by calyculi. Receptacles usually epaleate, rarely paleate. Heads liguliflorous. Corollas all ligulate (strap-shaped and 5-toothed)—yellow/orange, cyanic, or white. Anthers calcarate, tailed to sagittate—pollen usually lophate (with geometric patterns of spiny ridges). Style branches abaxially hispidulous, stigmatic areas continuous, apices usually acute (Figs. 8–9). Cypselae columnar, prismatic, fusiform, compressed, or obcompressed—often beaked. Pappi usually of bristles, bristles often plumose; sometimes of scales.

Lactuceae corresponds to Group 7 of *JepsMan* (p. 180–181).

II.D. **Vernonieae.**

No members of the tribe were treated in *JepsMan*.

II.E. **Liabeae.**

No members of the tribe were treated in *JepsMan*.

II.F. **Arctoteae.**

Herbs. Leaves basal and/or cauline; alternate—often pinnately lobed. Phyllaries in 3–5+ series, unequal—often scarious-margined. Receptacles epaleate, sometimes bristly. Heads radiate. Corollas zygomorphic or actinomorphic with short to long lobes—yellow/orange, cyanic, or white. Anthers calcarate, not tailed. Styles dilated distally, branches short, stigmatic areas continuous (Figs. 10–11). Cypselae obovoid, sometimes compressed—often shaggily villous, sometimes winged. Pappi of scales and/or bristles.

Key to genera treated in *JepsMan*

1. Phyllaries basally connate $\frac{1}{2}$ or more their lengths; laminae of ray corollas 5-nerved, 4-lobed or 4-toothed. *Gazania*
- 1' Phyllaries free to base or nearly so; laminae of ray corollas 4-nerved, 3-lobed or 3-toothed.
 2. Corollas of fresh ray florets whitish or purplish; pappi of conspicuous, unobscured scales. *Arctotis*
 - 2' Corollas of fresh ray florets yellow to orange; pappi none or minute or obscured by woolly hairs of cypselae.
 3. Fresh ray corollas uniformly yellow (drying bluish distally); cypselae woolly. *Arctotheca*
 - 3' Fresh ray corollas yellow to orange with purple at base; cypselae glabrous. *Venidium*

III.A. Inuleae.

Herbs. Leaves cauline; alternate. Phyllaries in 3–5+ series, unequal—usually chartaceous. Receptacles usually epaleate. Heads radiate. Corollas zygomorphic or actinomorphic with short lobes—yellow/orange, cyanic, or white. Anthers ecalcarate, tailed. Style branches linear, stigmatic in 2, distally confluent lines, rounded (Fig. 12). Cypselae columnar to prismatic—often ribbed. Pappi of scales and/or bristles.

Pulicaria paludosa Link is the only member of Inuleae s.s. treated in *JepsMan*.

Since *JepsMan* was published, *Dittrichia graveolens* (L.) Greuter [*Inula graveolens* (L.) Desf.] has been recorded as ruderal in \pm wet places near San Francisco Bay in sw Alameda and adjacent Santa Clara counties. The plants are erect, densely glandular (strongly scented) annuals, 2–5+ dm tall, with leaves alternate, leaf blades narrowly lanceolate to oblanceolate, 25–75 mm long, involucre obconic to campanulate, 4–7 mm high, ray corollas yellow, 2–5+ mm long, and pappi of ca. 30 bristles.

III.B. Plucheeae.

Shrubs, coarse herbs. Leaves cauline; alternate. Phyllaries in 3–5+ series, unequal—herbaceous or chartaceous. Receptacles epaleate. Heads disciform. Corollas actinomorphic with short lobes—usually cyanic or white, rarely yellow. Anthers ecalcarate, \pm tailed. Style branches oblong to linear, stigmatic in 2, ill-defined, distally confluent lines, abaxially papillate to hispidulous (Fig. 13). Cypselae \pm columnar to prismatic. Pappi of bristles.

Pluchea is the only genus of Plucheeae treated in *JepsMan*.

III.C. Gnaphalieae.

Mostly herbs—often <5 cm, often woolly. Leaves basal and/or cauline; alternate—entire, often decurrent onto stems. Phyllaries none, or 3–10 in 1–2 series, or 12–30 in 3–5+ series—often scarious-margined.

Receptacles paleate or epaleate. Heads discoid or disciform. Corollas actinomorphic with short lobes—yellow, cyanic, or white. Anthers ecalcarate, tailed. Style branches short to linear, stigmatic in 2, separate lines, obtuse or truncate (Fig. 14). Cypselae mostly obovoid, sometimes compressed. Pappi of free or basally connate bristles, the bristles sometimes plumose.

Key to genera treated in *JepsMan*

1. Plants unisexual or nearly so, the heads either with all or most florets pistillate or with all florets functionally staminate (pistillate heads rarely with 1–4 functionally staminate florets).
 2. Plants often stoloniferous, aerial stems mostly 1–2(–4) dm long; leaves of basal rosettes persisting through anthesis; cauline leaves mostly reduced. *Antennaria*
 - 2' Plants rhizomatous, aerial stems mostly 2–12 dm long; leaves of basal rosettes withering before anthesis; cauline leaves well-developed. *Anaphalis*
- 1' Plants not unisexual, the heads all \pm alike, each with 4–100+ pistillate and 2–20 functionally staminate or bisexual florets.
 3. Annuals or perennials, aerial stems to 120 cm long; phyllaries mostly 20–50+, imbricate in 3–6+ series; receptacles epaleate.
 4. Leaves often sessile, blade lengths mostly 3–5+ times widths; pistillate florets in each head usually far more numerous than bisexual florets. *Gnaphalium*
 - 4' Leaves petiolate, blade lengths 1–1.5 times widths; pistillate florets in each head usually fewer than bisexual florets.
 . . . *Helichrysum petiolare* Hilliard & B. L. Burtt. [Subshrubs, leaf blades rounded-deltate to ovate, 25–40 mm long, 20–35 mm wide, triplinerved, abaxially lanate, adaxially loosely tomentose, heads 40–60+ in crowded, corymbiform clusters, phyllaries chalky white; South African, locally naturalized in Marin County; not in *JepsMan*; noted by J. T. Howell (1970), as *Helichrysum petiolatum* (L.) DC.]
 - 3' Annuals, aerial stems to 20(–55) cm long; phyllaries none or 3–6 in 1(–2) series; receptacles paleate or not.
 5. Leaves mostly cauline and opposite. *Psilocarphus*
 - 5' Leaves mostly basal or alternate.
 6. Paleae \pm plane to concave, persistent. *Hesperervax*
 - 6' Paleae conduplicate, each falling with a cypsel.
 7. Inner florets bisexual, their cypselae pappose. *Filago*
 - 7' Inner florets functionally staminate, their ovaries mostly epappose.
 8. Innermost paleae with hardened, uncinat tips.
 *Ancistrocarphus*
 - 8' Innermost paleae similar to the outer or reduced, not uncinat at tip.
 9. Stems branched mostly from the base; style insertion terminal. *Stylocline*
 - 9' Stems branched distally or not at all; style insertion lateral. *Micropus*

III.D. Calenduleae.

Herbs. Leaves cauline; alternate. Phyllaries in 1–2 series, \pm equal—herbaceous. Receptacles epaleate. Heads radiate. Corollas zygomorphic or actinomorphic with short lobes—yellow/orange, cyanic,

or white. Anthers ecalcarate, tailed. Style branches stout to linear, stigmatic in 2, distally confluent lines, apically \pm truncate to deltoid (Figs. 15–16). Cypselae variously straight or coiled—usually ornamented with prickles, ridges, or wings. Pappi none.

Key to genera treated in *JepsMan*

1. Disc florets bisexual, fertile. *Dimorphotheca*
- 1' Disc florets functionally staminate.
 2. Ray corollas yellow to orange; cypselae incurved or coiled, abaxially prickly or warty. *Calendula*
 - 2' Ray corollas purplish or whitish; cypselae straight, smooth or somewhat sculptured with wavy ridges. *Osteospermum*

III.E. **Astereae.**

Shrubs, herbs. Leaves basal and/or cauline; alternate. Phyllaries usually in 3–5+ series, unequal, sometimes in 1–2 series, subequal. Receptacles epaleate, with few exceptions. Heads radiate, discoid, or disciform. Corollas zygomorphic or actinomorphic with short lobes (rarely long)—yellow (rarely orange), cyanic, or white. Anthers ecalcarate, not tailed. Style branches linear, stigmatic in 2, separate lines, adaxial faces of appendages smooth, glabrous (Figs. 17–19). Cypselae mostly obconic to obpyramidal, sometimes compressed. Pappi usually of bristles, sometimes scales or of scales and bristles, rarely none.

Key to genera treated in *JepsMan*

1. Plants unisexual, florets in each head either all pistillate (rarely with rudimentary anthers) or all functionally staminate. *Baccharis*
- 1' Plants not unisexual, not with florets of each head all pistillate or all functionally staminate (rarely some heads with all florets functionally staminate).
2. Phyllaries equal or subequal in 1–2(–3) series.
 3. Plants scapiform herbs; receptacles conic; pappi none. *Bellis*
 - 3' Plants mostly not scapiform; receptacles mostly flat to convex; pappi usually present in most species.
 4. Pappi wholly or mostly of scales (scales subulate in some spp., see couplets 5 and 6), or an erose crown, or none (then see couplets 5 and 6).
 5. Ray florets 10–20, corollas mostly showy, white or cyanic; pappi coronas or of free or connate, erose to lacinate scales plus (0–)1–12 bristles. *Monoptilon*
 - 5' Ray florets 5–15, corollas inconspicuous, yellow, sometimes tinged with purple; pappi none or of (1–)5 subulate scales. *Rigiopappus*
 - 4' Pappi wholly or mostly of bristles (pappus sometimes none or subulate scales in *Pentachaeta* spp.; see couplet 6).
 6. Annuals; leaves linear, entire; pappi none or of 3–20 bristles or subulate scales. *Pentachaeta*
 - 6' Annuals or perennials; leaves mostly broader, entire, toothed, or pinnatifid; pappi of (5–)20–60+ bristles.
 7. Annuals or perennials; heads radiate or discoid, not dis-

- ciform, corollas of ray florets with \pm conspicuous laminae (1–)3–15+ mm long; disc florets mostly 20–100+ per head. *Erigeron* p.p.
- 7' Annuals; heads mostly disciform (if radiate, the rays inconspicuous, laminae less than 1 mm long); disc florets mostly 5–12(–20) per head. *Conyza*
- 2' Phyllaries unequal, graduated in 3–6+ series.
8. Pappi wholly or mostly of scales (scales subulate to setiform in some spp.; see couplets 9 and 11).
9. Ray florets 12–100 per head, corollas white or cyanic. *Townsendia*
- 9' Ray florets none or 1–60 per head, corollas yellow.
10. Receptacles paleate. *Eastwoodia*
- 10' Receptacles epaleate.
11. Disc florets functionally staminate; cypselae (ray) compressed or flattened with pappi of 5–20 simple or laciniate, free or connate scales (pappus scales of disc ovaries subulate or setiform, often hispidulous, often twisted or contorted). *Amphipappus*
- 11' Disc florets bisexual, fertile; cypselae not compressed or flattened; pappus scales not hispidulous, not twisted or contorted.
12. Leaves mostly serrate to dentate, rarely entire; phyllary tips spreading to recurved or coiled in most spp.; cypselae glabrous; pappus scales usually falling readily. *Grindelia*
- 12' Leaves entire; phyllary tips \pm appressed; cypselae hairy; pappus scales \pm persistent.
13. Involucres \pm cylindric to obconic or turbinate; disc florets 1–13 per head. *Gutierrezia*
- 13' Involucres hemispheric; disc florets 13–80 per head. *Acamptopappus*
- 8' Pappi wholly or mostly of bristles (with shorter, outer scales or setae in some spp.; sometimes wholly of subulate scales in *Lessingia*, see couplet 14).
14. Annuals; heads mostly radiant (all florets bisexual, corollas of 1 or more peripheral florets palmately cleft, zygomorphic; such corollas usually larger than those of more central florets); corollas cyanic in most spp., (yellow in some spp., then often tinged with purple). *Lessingia* p.p.
- 14' Mostly perennials, some annuals; heads disciform, discoid, or radiate, not radiant; disc corollas yellow in most spp., rarely tinged with purple (whitish in some members of *Chrysothamnus*; see couplet 22).
15. Heads discoid (florets all bisexual and fertile; corollas all actinomorphic).
16. Throats of corollas abruptly dilated at base. . . . *Isocoma*
- 16' Throats of corollas gradually, if at all, dilated.
17. Cypselae 5-angled, glabrous, 5–10 mm long. *Hazardia* p.p.
- 17' Cypselae flat, compressed, obconic, obpyramidal, or \pm cylindric in most spp., rarely 5-angled, hairy in most spp., 1–4 mm long.
18. Cypselae flat or \pm compressed.

- 19. Cypselae with 5–7 ribs on each face. . . .
 *Machaeranthera* p.p.
- 19' Cypselae not with 5–7 ribs on each face.
 - 20. Plants mostly rhizomatous, some taprooted; variously glabrous or hairy, surfaces of the hairs smooth.
 *Erigeron* p.p.
 - 20' Plants taprooted; most plants strigose, surfaces of the hairs knobby or verrucose. *Heterotheca* p.p.
- 18' Cypselae not compressed.
 - 21. Plants herbaceous, aerial stems from rhizomes or caudices. *Aster* p.p.
 - 21' Plants suffrutescent or shrubby, aerial stems from taproots.
 - 22. Involucres cylindric or narrowly obpyramidal in most spp.; phyllaries mostly in 4–5 ranks, each phyllary usually keeled or medially gland-thickened, at least distally; florets 2–5(–20) per head. *Chrysothamnus*
 - 22' Involucres mostly obconic to hemispheric; phyllaries spirally arranged, seldom keeled or gland-thickened; florets (4–) 10–25(–70) per head. *Ericameria* p.p.
- 15' Heads radiate (peripheral, ray, florets pistillate or neuter, corollas of ray florets with laminae 1.5–30+ mm long). . . .
 **Go to couplet 23**
- 23. Corollas of ray florets white or cyanic.
 - 24. Caespitose herbs or subshrubs; phyllary margins translucent.
 *Chaetopappa*
 - 24' Habits various, caespitose in very few spp.; phyllary margins not translucent in most spp.
 - 25. Coarse, rhizomatous, colonial herbs or subshrubs, often thorny; leaves linear and soon falling, or persistent and scale-like. *Chloracantha*
 - 25' Habits various, not thorny; leaves not soon falling, not scale-like.
 - 26. Leaves mostly serrate to pinnatifid, the teeth or lobes often bristle-tipped; phyllaries usually whitish to stramineous and \pm chartaceous proximally, green and herbaceous distally (rarely herbaceous throughout).
 - 27. Mostly herbs; heads mostly in loose, corymbiform clusters; involucres mostly 3–12(–15) mm high; laminae of ray corollas 7–15(–20) mm long. *Machaeranthera* p.p.
 - 27' Mostly shrubs or subshrubs; heads mostly solitary; involucres mostly 13–19 mm high; laminae of ray corollas (10–)15–30+ mm long. *Xylorhiza*
 - 26' Leaves entire to serrate, the teeth not bristle-tipped; phyllaries mostly uniformly herbaceous (herbaceous medially and distally and chartaceous only laterally at the base in some spp.).
 - 28. Phyllaries (all or at least some) each marked with 3 orange veins (at least near base). *Trimorpha*
 - 28' Phyllaries not marked with 3 orange veins (sometimes 1 orange vein in each phyllary in some spp.).

29. Phyllaries mostly lanceolate to linear, not thickened distally; style branch appendages shorter than stigmatic areas in most spp.; pappi double (with short, outer setae subtending the primary bristles) in many spp. *Erigeron* p.p.
- 29' Phyllaries mostly oblanceolate or broader, often thickened distally; style branch appendages longer than stigmatic areas, or at least longer than wide, in most spp.; pappi simple (without outer setae) in most spp.
30. Stems usually \pm tomentose; ray florets neuter; pappi reddish. *Lessingia* p.p.
- 30' Stems seldom, if ever, tomentose; ray florets pistillate, fertile; pappi seldom reddish. *Aster* p.p.
- 23' Corollas of ray florets yellow in most spp., pale or tinged with purple in some spp.
31. Disc florets all functionally staminate.
32. Annuals; ray florets 5–8 per head; pappi of 2–8 fragile bristles. *Lessingia* p.p.
- 32' Perennials; ray florets 1–3 per head; pappi of 20+ persistent bristles. *Petradoria*
- 31' Disc florets all or mostly bisexual and fertile (the innermost sometimes functionally staminate in *Prionopsis*; see couplet 39).
33. Pappus bristles (disc; ray cypselae often epappose) subtended by scales or setae to 1 mm long. *Heterotheca* p.p.
- 33' Pappus bristles (disc and ray) subequal or intergrading in most spp., the outer seldom shorter than and contrasting with the inner.
34. Habit annual; cypselae fusiform, distally rostrate or beaked. *Tracynia*
- 34' Habit perennial in most spp., annual in some spp.; cypselae not fusiform, not rostrate or beaked.
35. Shrubs with entire leaves. *Ericameria* p.p.
- 35' Herbs or, if shrubby, leaves mostly serrate.
36. Perennials, from rhizomes or caudices.
37. Leaves mostly spatulate to ovate, serrate or entire, not resin-gland-dotted; heads often in secund, racemiform clusters; ray florets mostly 3–15(–21) per head. *Solidago*
- 37' Leaves mostly linear, entire, sometimes resin-gland-dotted; heads solitary or in corymbiform clusters; ray florets mostly 15–38 per head.
38. Heads in corymbiform clusters; ray florets 15–25 per head; disc florets 6–15 per head. *Euthamia*
- 38' Heads solitary; ray florets 25–38 per head; disc florets mostly 30–60+ per head. *Erigeron* p.p.
- 36' Perennials (some with branched caudices; see couplet 42), biennials, and annuals from taproots.
39. Annuals, biennials, or short-lived perennials, mostly herbs; leaves serrate to pinnatifid, the teeth or lobes bristle-tipped.
40. Cypselae hairy (ray and disc); pappus bristles \pm free to base, persistent. *Machaeranthera* p.p.
- 40' Cypselae mostly glabrous (those of disc sometimes puberulent); pappus bristles \pm connate at base, falling \pm together, \pm readily. *Prionopsis*

- 39' Perennials, herbs, subshrubs, or shrubs; leaves entire or toothed, the teeth not bristle-tipped in most spp. (if bristle-tipped, see couplet 42).
- 41. Stems \pm prostrate, plants mat-forming; leaves clustered at ends of stems; heads solitary on erect, \pm naked peduncles. *Stenotus*
- 41' Stems decumbent to erect, plants seldom mat-forming; leaves not clustered at ends of stems; heads 1–5+ on leafy stems or bracteate peduncles.
- 42. Shrubs or subshrubs, stems 2–25 dm long; leaves mostly cauline, sometimes with bristle-tipped teeth. *Hazardia* p.p.
- 42' Herbs from woody taproots or branched caudices, stems 5–90 cm long; leaves both basal and cauline or mostly basal, seldom with bristle-tipped teeth.
- 43. Leaves and/or stems loosely tomentose to woolly in most spp., glandular-punctate in some spp., \pm glabrous in some spp., stipitate-glandular (only distally) in some spp.; cypselae obpyramidal, 3–4-angled. *Pyrrocoma*
- 43' Leaves and stems densely stipitate-glandular, \pm viscid throughout or nearly so; cypselae various shapes, not obpyramidal, not 3–4-angled. *Tonestus*

III.F. Anthemideae.

Herbs, rarely subshrubs or shrubs. Leaves mostly cauline, sometimes basal; alternate—often finely dissected, usually strong-scented. Phyllaries in 3–5 series, unequal—scarious-margined. Receptacles paleate or epaleate—sometimes hairy. Heads radiate, discoid, or disciform. Corollas zygomorphic or actinomorphic with short lobes—yellow, cyanic, or white. Anthers ecalcarate, not tailed. Style branches linear, stigmatic in 2, separate lines, usually truncate (Figs. 20–21). Cypselae columnar to prismatic, sometimes compressed—sometimes ribbed or winged. Pappi usually none, sometimes of scales or coroniform—never of bristles.

Key to genera treated in *JepsMan*

- 1. Heads radiate.
- 2. Receptacles paleate.
 - 3. Capitulescences mostly of 12–50+ heads in close, corymbiform clusters; ray florets 3–8 per head. *Achillea*
 - 3' Capitulescences of 2–10 heads in loose, cymiform clusters or heads solitary; ray florets 10–25 per head.
 - 4. Cypselae 10-ribbed. *Anthemis*
 - 4' Cypselae 2–3-striate or weakly 2–3-ribbed. . . . *Chamaemelum*
- 2' Receptacles epaleate.
 - 5. Cypselae all 5–10-ribbed, none winged.
 - 6. Laminae of ray corollas 10–40+ mm long. . . . *Leucanthemum*
 - 6' Laminae of ray corollas 5–8 mm long. *Tanacetum* p.p.

- 5' Cypselae of rays 1-4-winged, those of the disc winged or not.
- 7. Shrubs or subshrubs; ray corollas white in most spp. *Argyranthemum*
- 7' Annuals; ray corollas yellow to orange in most spp., white with red or purple base in very few spp.
- 8. Plants \pm glabrous; wings of cypselae not ending in spine-like processes. *Chrysanthemum*
- 8' Plants viscid; wings of cypselae distally firm and sharp, spine-like. *Heteranthemis*
- 1' Heads discoid or disciform (peripheral, pistillate florets may lack corollas).
- 9. Heads discoid, all florets bisexual.
- 10. Receptacles convex, paleate; cypselae 3-5-angled. *Santolina*
- 10' Receptacles \pm conic, epaleate; cypselae ovoid and smooth or weakly obcompressed and obscurely 5-ribbed on adaxial faces.
- 11. Shrubs and coarse herbs; capitulescences racemiform or paniculiform; florets 3-30 per head. . . . *Artemisia* p.p. (*Seriphidium*)
- 11' Annuals; capitulescences of solitary or loosely clustered heads; florets 50-150+ per head. *Chamomilla* (*Matricaria*)
- 9' Heads disciform, peripheral florets pistillate.
- 12. Pistillate florets lacking corollas.
- 13. Heads pedunculate. *Cotula*
- 13' Heads sessile in leaf axils. *Soliva*
- 12' Pistillate florets all with corollas.
- 14. Capitulescences usually tightly corymbiform, sometimes loosely corymbiform; receptacles convex; pappi usually present, coroniform. *Tanacetum* p.p.
- 14' Capitulescences paniculiform, racemiform, or spiciform, or heads solitary in most spp., corymbiform in very few spp.; receptacles hemispheric to conic; pappi mostly none.
- 15. Heads mostly 20-200+ per capitulescence; florets 3-25(-60+) per head. *Artemisia* s.s.
- 15' Heads mostly 1-10 per capitulescence; florets mostly 30-50 per head. *Sphaeromeria*

III.G. Senecioneae.

Shrubs, herbs. Leaves basal and/or cauline; alternate—pinnately divided, toothed, or entire. Phyllaries usually in 1-2 series, subequal (3-5-seriate, unequal in *Lepidospartum*)—sometimes subtended by calyculi. Receptacles epaleate. Heads radiate, discoid, or disciform. Corollas zygomorphic or actinomorphic with short lobes—usually yellow, rarely orange, cyanic, or white. Anthers ecalcarate, not tailed. Style branches linear, stigmatic in 2, separate lines, usually truncate, sometimes appendaged (Figs. 14, 22-23). Cypselae obovoid, columnar, or prismatic. Pappi usually of fine bristles, rarely of subulate scales, the elements never plumose.

Key to genera treated in *JepsMan*

- 1. Receptacles hemispheric to conic; cypselae usually with myxogenic hairs or papillae (exuding mucilage after being wetted).
- 2. Ray corollas with very short or no tube; disc florets functionally staminate; pappi none. *Blennosperma*

- 2' Ray corollas with distinct tube; disc florets bisexual; pappi of fine bristles.
..... *Crocidium*
- 1' Receptacles flat to convex; cypselae glabrous or variously hairy, not with myxogenic hairs or papillae.
 - 3. Corollas whitish to purplish; anther-bearing florets functionally staminate.
..... *Petasites*
 - 3' Corollas yellow in most spp., white, ochroleucous, or purple in few spp.; anther-bearing florets bisexual.
 - 4. Heads radiate. *Senecio* p.p.
 - 4' Heads discoid or disciform.
 - 5. Heads disciform. *Erechtites*
 - 5' Heads discoid.
 - 6. Herbs (never climbing).
 - 7. Leaves palmately veined and lobed. *Cacaliopsis*
 - 7' Leaves pinnately veined (or 1-nerved).
 - 8. Leaves variously hairy, not both densely white-tomentose abaxially and glabrous-shiny adaxially; involucre often calyculate; phyllaries often black-tipped; style branches truncate-penicillate.
..... *Senecio* p.p.
 - 8' Leaves abaxially densely white-tomentose, adaxially glabrous-shiny; involucre not calyculate; phyllaries not black-tipped; style branches rounded-truncate. ...
..... *Luina*
 - 6' Shrubs or vines.
 - 9. Vines; leaves \pm palmately lobed. *Senecio* p.p.
 - 9' Shrubs; leaves not palmately lobed, mostly spatulate to oblanceolate, or linear to filiform, or scale-like.
 - 10. Capitulescences umbelliform or heads solitary; phyllaries 4–5(–9), subequal in 1–2 series. *Tetradymia*
 - 10' Capitulescences paniculiform; phyllaries 8–23, graduated in 3–5+ series. *Lepidospartum*

III.H. *Heliantheae*.

Shrubs, herbs. Leaves basal and/or cauline; opposite or alternate—blades pinnately divided, toothed, or entire. Phyllaries in 1–2 series and subequal or 3–5+ series and unequal—rarely subtended by calyculi. Receptacles paleate or epaleate. Heads radiate, discoid, disciform, or radiant. Corollas zygomorphic or actinomorphic, usually with short lobes—usually yellow/orange, rarely cyanic or white. Anthers ecalcarate, not tailed. Style branches linear, usually stigmatic in 2, separate lines (sometimes stigmatic areas continuous), adaxial faces of appendages papillate or hairy (Figs. 23–26). Cypselae obovoid, columnar, prismatic, or fusiform, often weakly to strongly compressed or obcompressed, sometimes winged. Pappi usually of scales, sometimes of scales and bristles or wholly of bristles or none—bristles rarely plumose.

Key to subtribes for genera treated in *JepsMan*

- 1. Heads unisexual in most spp.; pistillate florets without corollas in most spp.; anthers free in most spp. (filaments connate in some spp.). *Ambrosiinae*

- 1' Heads not unisexual; pistillate florets bearing corollas in nearly all spp.; anthers connate (filaments not connate).
2. Leaves and/or phyllaries dotted or streaked with pellucid, schizogenous glands containing strong-scented oils. Pectidinae
- 2' Leaves and/or phyllaries rarely streaked or dotted, never with pellucid, schizogenous glands containing strong-scented oils (plants may have sessile or stipitate, surface glands and may be otherwise strong-scented, e.g., from sesquiterpene-lactones; pellucid streaks of some Coreopsidinae do not contain strong-scented oils).
3. Receptacles wholly or partially paleate (i.e., at least one series of paleae between ray florets and disc florets).
4. Plants with tack-glands or pit-glands on stems, leaves, and/or phyllaries in some species; phyllaries in 1+ series, each phyllary wholly or partially investing the ovary of a subtended floret in most spp.; paleae restricted to a single series at periphery of head in most spp., often connate in a ring (each disc floret subtended by a palea in very few spp.); laminae of ray corollas often flabellate, deeply lobed; pappus elements various, sometimes coarse, plumose or woolly bristles or subulate, plumose or woolly scales. . . . Madiinae
- 4' Plants without tack-glands or pit glands; phyllaries in (1-)2-7+ series, each inner phyllary wholly or partially investing the ovary of a subtended floret in very few spp.; paleae not restricted to periphery of head, all or nearly all disc florets subtended by paleae; laminae of ray corollas seldom flabellate or deeply lobed; pappus elements various, plumose in very few spp.
5. Phyllaries in 2-3 series, those of the single outer series often shorter than and contrasting sharply with those of the 1-2 inner series (the outer series often termed a calyculus); disc cypselae obcompressed or quadrangular-fusiform. . . . Coreopsidinae
- 5' Phyllaries in 1-6+ series, the outer \pm similar to or intergrading with the inner; disc cypselae seldom obcompressed or quadrangular-fusiform.
6. Phyllaries falling with the cypselae in fruit; ray florets (if any) pistillate and fertile.
7. Anther thecae pale; pappi of \pm plumose, subulate scales or bristles. . . . Galinsoginae p.p. (*Galinsoga*)
- 7' Anther thecae black; pappi none. Milleriinae.
- 6' Phyllaries persistent in fruit; ray florets (if any) pistillate and fertile, or styliferous and sterile, or neuter.
8. Receptacles spheric to high-conic or columnar, mostly 8-20+ mm high. Rudbeckiinae
- 8' Receptacles mostly flat to convex or conic, mostly less than 5 mm high.
9. Leaves mostly cauline and alternate (none or only the proximal opposite); ray florets neuter, or styliferous and sterile; pappi, if present, of fragile or caducous scales or awns. Helianthinae
- 9' Leaves mostly basal or opposite, sometimes alternate; ray florets pistillate and fertile in most spp. (if neuter, leaves mostly basal or alternate); pappi present and persistent in most spp.: scales, awns, and/or bristles.
10. Heads discoid; pappi of 15-30 \pm plumose bristles or subulate scales.
. Galinsoginae p.p. (*Bebbia*)

- 10' Heads radiate or discoid; pappi none or of 2(–8) non-plumose scales. Ecliptinae
- 3' Receptacles wholly epaleate in most spp., rarely bearing setiform or conic enations (Gaillardinae, *Gaillardia*) or \pm membranous paleae (Chaenactidinae, *Chaenactis carphoclinia*); see also, first lead of couplet 4 (Madiinae).
- 11. Stems to 5 cm long; phyllaries 2–3; florets 2–3 in each head; pappi of ca. 20 subulate, plumose, basally connate scales. Dimeresiinae
- 11' Stems mostly more than 5 cm long; phyllaries 2–50+; florets 2–100+ in each head; pappi none or of nonplumose bristles and/or scales in most spp.
- 12. Leaves opposite, oblong to linear or filiform, sessile or nearly so, often somewhat succulent; cypselae cylindric to clavate and 8–15-ribbed.
- 13. Plants usually erect, seldom rooting at nodes; phyllaries 2–5, subequal, in 1 series. Flaveriinae
- 13' Plants prostrate, rooting at nodes; phyllaries 12–15+, graduated, in 3+ series. Jaumeinae
- 12' Leaves various; cypselae various, not both cylindric to clavate and 8–15-ribbed (cylindric and 5–10-nerved in some *Arnica* spp., in Chaenactidinae).
- 14. Phyllaries \pm navicular; disc corollas usually 4-lobed; cypselae strongly compressed, callous-margined, often ciliate. Peritylinae
- 14' Phyllaries flat to \pm concave or weakly navicular; disc corollas (4–)5-lobed; cypselae various (strongly compressed and callous-margined or ciliate in very few spp.).
- 15. Cypselae stoutly obconic to obpyramidal, length seldom more than 2.5(–3.5) times the thickness in most spp.
- 16. Phyllaries mostly not scarious-margined; disc corollas often with moniliform hairs on tube, throat, and/or lobes; cypselae not both 4-angled and 12–16-ribbed. Gaillardinae
- 16' Phyllaries notably scarious-margined; disc corollas without moniliform hairs; cypselae mostly 4-angled and 12–16-ribbed. Hymenopappinae
- 15' Cypselae narrowly obconic or obpyramidal to clavate or columnar, length more than 3.5 times the thickness in most spp. (if shorter, then \pm compressed).
- 17. Leaves sessile in most spp., obscurely petiolate in few spp., rarely truly petiolate; pappus scales, if any, not medially thickened. Baeriinae
- 17' Leaves clearly petiolate in most spp. (\pm sessile in some spp. of *Arnica*, *Chaenactis*, *Hulsea*); pappus scales, if any, notably medially thickened in most spp. Chaenactidinae

Heliantheae—Ambrosiinae

- 1. Pistillate and functionally staminate florets together in same head (some spp. with some heads staminate); cypselae not enclosed in perigynia (nut-like or bur-like structures).
- 2. Cypselae obcompressed or not, without wing-like margins. *Iva*

- 2' Cypselae strongly obcompressed and with toothed or lobed, wing-like margins. *Dicoria*
- 1' Pistillate and functionally staminate florets in separate heads; cypselae enclosed within hardened, often prickly, tuberculate, or winged, perigynia.
- 3. Phyllaries of staminate heads free to base, receptacles conic. *Xanthium*
- 3' Phyllaries of staminate heads partially or wholly connate, receptacles flat or convex.
- 4. Perigynia prickly, tuberculate, or unarmed. *Ambrosia*
- 4' Perigynia bearing 5–15+ scarious, cuneate to flabellate wings. *Hymenoclea*

Heliantheae—Baeriinae

- 1. Leaves all or mostly opposite. *Lasthenia*
- 1' Leaves mostly alternate (proximal leaves opposite or in rosettes in few spp.).
- 2. Plants glabrous or granular-glandular, not at all woolly. *Amblyopappus*
- 2' Plants sparsely to densely woolly on stems and/or leaves and/or phyllaries.
- 3. Heads disciform (4–7 peripheral florets pistillate, with tubular corollas) or inconspicuously radiate. *Lembertia*
- 3' Heads conspicuously radiate or truly discoid.
- 4. Phyllaries becoming reflexed in fruit. *Eatonella*
- 4' Phyllaries not reflexed in fruit.
- 5. Ray corollas obscurely bilabiate, with a minute adaxial lobe opposite the lamina. *Monolopia*
- 5' Ray corollas not bilabiate, or rays none.
- 6. Annuals or perennials; corollas without rings of hairs at bases of limbs; ray cypselae prismatic, 4–5-angled in most spp. *Eriophyllum*
- 6' Annuals; corollas each with a ring of hairs at base of limb; ray cypselae \pm obcompressed. *Pseudobahia*

Heliantheae—Chaenactidinae

- 1. Pappi wholly or partially of bristles (pappi none and ray corollas whitish with red veins in *Syntrichopappus lemmonii*; see couplet 3).
- 2. Leaves all or mostly opposite. *Arnica*
- 2' Leaves mostly basal or alternate.
- 3. Shrubs; leaves linear-filiform. *Peucephyllum*
- 3' Herbs; leaves not linear-filiform. *Syntrichopappus*
- 1' Pappi none or wholly of scales; all, some, or none of the scales aristate.
- 4. Leaves all or mostly cauline and all or mostly opposite (some spp. with few distal leaves alternate).
- 5. Ray corollas persistent, becoming papery; disc florets usually functionally staminate; cypselae obovoid or plumply fusiform, smooth or ca. 20-ribbed. *Whitneya*
- 5' Ray corollas withering, not becoming papery, or rays wanting; disc florets bisexual, fertile; cypselae obpyramidal, usually 4-angled.
- 6. Phyllaries 4–9(–12), margins usually purplish or yellowish. *Schkuhria*
- 6' Phyllaries (5–)8–21+, margins not purplish or yellowish. *Bahia* p.p.
- 4' Leaves all or mostly basal, or mostly cauline and mostly alternate (some spp. with few proximal leaves opposite).
- 7. Phyllaries unequal, the outer foliaceous, rotund to broadly ovate, spreading or reflexed. *Venegasia*

- 7' Phyllaries subequal, all linear or lanceolate to spatulate or oblanceolate, appressed.
- 8. Disc corolla lobes lance-linear to linear, length mostly 2 or more times width.
 - 9. Pappus scales 12–18. *Hymenothrix*
 - 9' Pappus scales 4–10. *Palafoxia*
- 8' Disc corolla lobes deltate to lance-deltate or ovate, length mostly less than 2 times width (sometimes more in zygomorphic corollas of some *Chaenactis* spp.; see couplet 11).
- 10. Stems and/or leaves sparsely to densely hairy with white, straight, often conic or fusiform, hairs 0.1–0.8 mm long in most spp., not cobwebby or woolly, some spp. glabrous, some spp. stipitate-glandular, most spp. glandular-punctate or resin-gland-dotted; cypselae obpyramidal, sharply 4–5-angled. *Bahia* p.p.
- 10' Stems and/or leaves thinly cobwebby to densely woolly with crisped, tangled, or matted hairs more than 0.8 mm long, or finely granular-pubescent with bulbous hairs less than 0.2 mm long, or glabrous, some spp. stipitate-glandular or glandular-punctate; cypselae obconic, clavate, or linear, often compressed, obscurely, if at all, 4–5-angled.
 - 11. Ray florets 9–60+. *Hulsea*
 - 11' Ray florets none (corollas of peripheral florets sometimes zygomorphic and larger than the inner ones).
 - 12. Capitulescences loosely corymbiform or heads solitary; disc florets 8–40+. *Chaenactis*
 - 12' Capitulescences tightly corymbiform or glomerulate; disc florets 4–9. *Orochaenactis*

Heliantheae—Coreopsidinae

- 1. Principal phyllaries connate 1/5–7/8 their lengths. *Thelesperma*
- 1' Principal phyllaries free to the base, or nearly so.
 - 2. No cypselae strongly 4-angled, all strongly obcompressed, none distally attenuate or beaked.
 - 3. Cypselae orbicular to linear-ovate, usually all within a head ± winged; pappi not of retrorsely barbed awns. *Coreopsis*
 - 3' Cypselae cuneate or linear to spatulate, few, if any, within a head winged; pappi usually of retrorsely barbed awns. *Bidens* p.p.
 - 2' At least innermost cypselae 4-angled, sulcate on the faces, distally attenuate or beaked.
 - 4. Paleae mostly persistent on receptacles; peripheral cypselae mostly much shorter and flatter than the slender, more attenuate inner ones. *Bidens* p.p.
 - 4' Paleae mostly not persistent, commonly falling with the cypselae; cypselae within a head all more-or-less the same shape and intergrading in length. *Cosmos*

Heliantheae—Dimeresiinae

Dimeresia is the only genus in Dimeresiinae.

Heliantheae—Ecliptinae

- 1. Ray corollas sessile, persistent, and becoming papery. *Sanvitalia*
- 1' Ray corollas seldom sessile (i.e., typically the lamina borne on a tube), never persistent and becoming papery, rarely wanting.

2. Receptacular paleae linear-filiform, not conduplicate; corollas of ray and disc florets whitish. *Eclipta*
- 2' Receptacular paleae lanceolate to ovate, conduplicate; corollas of ray and disc florets yellow to orange.
3. Cypselae prismatic, or nearly so, 3–4-angled.
 4. Cauline leaves well-developed; pappi none or 3–4 teeth or scales. . . . *Wyethia*
 - 4' Cauline leaves much reduced; pappi none. *Balsamorhiza*
- 3' Cypselae weakly compressed to strongly flattened, not at all prismatic.
 5. Some or all cypselae winged (i.e., each bordered by a wing of membranous or corky tissue different from that of the body of the cypselae); pappi of 2 persistent subulate or aristate scales or awns without any additional scales. *Verbesina*
 - 5' Cypselae sometimes sharp-edged but none truly winged; pappi various, rarely as above.
 6. Leaves all or mostly basal, scapiform herbs; involucre 20–30+ mm diam. *Enceliopsis*
 - 6' Leaves basal and cauline and mostly cauline, herbs or shrubs; involucre 4–30 mm diam.
 7. Basal leaves persisting; cypselae thin-edged, not white-margined or ciliolate. *Helianthella*
 - 7' Basal leaves ephemeral; cypselae white-margined and ciliolate.
 8. Shrubs. *Encelia*
 - 8' Herbs (annual or perennial). *Geraea*

Heliantheae—Flaveriinae

Flaveria is the only genus of Flaveriinae treated in *JepsMan*.

Heliantheae—Gaillardiiinae

1. Pappi of 35–140 free or basally connate bristles in 1–4 series. . . . *Psathyrotes*
- 1' Pappi none or of 2–12 subulate or broader scales.
 2. Pappus scales 5, ovate to flabellate, deeply and finely lacerate, each seemingly constituted of 8–15+ connate bristles. *Trichoptilium*
 - 2' Pappi none or of 2–12 scales, the scales not flabellate and finely lacerate, variously ovate or spatulate to lanceolate or subulate, entire, erose, or coarsely lacerate, often attenuate or uniaristate.
 3. Phyllaries strongly reflexed in fruit; receptacles mostly globose, with or without setiform enations; disc corollas often brown-purple or marked with brown-purple, with tube much shorter than the abruptly much-dilated, urceolate to campanulate throat, lobes often shaggily hairy with moniliform hairs.
 4. Leaves not linear-filiform or divided into linear-filiform lobes nor with bases decurrent on stems; receptacles usually bearing setiform enations. *Gaillardia*
 - 4' Leaves linear-filiform, or divided into linear-filiform lobes, or broader and not divided (then with bases strongly decurrent on stems); receptacles rarely bearing setiform enations. *Helenium*
 - 3' Phyllaries mostly erect to spreading in fruit; receptacles flat to ovoid, conic, domed, or hemispheric, variously smooth to pitted, without setiform enations; disc corollas uniformly yellow to cream or, sometimes, reddish, with tube much shorter than to about equalling the slightly dilated, funnelliform to cylindric throat, lobes not shaggily hairy with moniliform hairs.
 5. Corollas of ray florets withering (rarely none in *Hymenoxys*; see couplet 6), falling early or tardily.

- 6. Outer phyllaries connate 1/5–1/2+ their lengths. . . . *Hymenoxys* (s.s.)
- 6' Outer phyllaries free to the base or nearly so. *Dugaldia*
- 5' Corollas of ray florets persistent (rarely none in *Tetranneuris*; see couplet 8), becoming strongly reflexed and papery.
- 7. Pappi none. *Baileya*
- 7' Pappi of 4–6 scales.
- 8. Plants mostly scapiform with heads borne singly; involucre hemispheric to rotate; ray florets none or 5–21+; disc florets 25–150+. *Hymenoxys* (*Tetranneuris*)
- 8' Plants not scapiform, heads usually in close corymbiform or glomerulate clusters; involucre cylindric to campanulate; ray florets 2–7; disc florets 8–25+. *Psilostrophe*

Heliantheae—Galinsoginae

- 1. Annuals; cypselae of ray florets each shed together with a subtending phyllary and 2 adjacent paleae. *Galinsoga*
- 1' Perennials; cypselae shed separate from the phyllaries and the persistent or tardily falling receptacular paleae. *Bebbia*

Heliantheae—Helianthinae

- 1. Pappi present, caducous. *Helianthus*
- 1' Pappi none, or persistent or falling tardily.
- 2. Leaves mostly 3- or 5-nerved; phyllaries 12–21+ in 2–6+ series, subequal or strongly graduate, the outer ribbed, or keeled, or indurate at base; pappi present or absent. *Viguiera*
- 2' Leaves usually 1-nerved; phyllaries 12–21 in 2–3 series, mostly subequal, uniformly herbaceous; pappi none. *Helioneris*

Heliantheae—Hymenopappinae

Hymenopappus is the only genus of Hymenopappinae treated in *JepsMan*.

Heliantheae—Jaumeinae

Jaumea is the only genus of Jaumeinae treated in *JepsMan*.

Heliantheae—Madiinae

- 1. Cypselae all \pm cylindric, fusiform, or prismatic, sometimes 8–10-ribbed or -nerved, hairy in most species (if rays none, plants perennial).
- 2. Perennials.
 - 3. Plants mostly scapiform; leaves mostly basal. *Raillardella*
 - 3' Plants not scapiform; leaves mostly cauline. *Raillardopsis*
- 2' Annuals.
 - 4. Corollas yellow to red; pappi of 10, \pm spatulate, nonplumose scales, 5 shorter, alternating with 5 longer. *Achyraea*
 - 4' Corollas white (sometimes with reddish nerves); pappi none or of 12–20, subulate, ciliate to plumose scales.
 - 5. Leaves basal and cauline, the proximal usually toothed; receptacles with paleae in 1(–2) peripheral series; flowering mostly in fall. *Blepharizonia*

- 5' Leaves mostly cauline, entire; receptacles paleate throughout; flowering mostly in late spring. *Blepharipappus*
- 1' Cypselae of ray florets \pm obcompressed, or laterally compressed, or stoutly obovoid, never 8–10-ribbed, usually glabrous (if rays none, plants annual).
6. Involucres closely subtended by 3–6 caducous, phyllary-like bractlets; disc florets 3–6, functionally staminate. *Lagophylla*
- 6' Involucres not closely subtended by caducous bractlets; disc florets 1–60+, usually bisexual and fertile (if functionally staminate, usually more than 6).
7. Leaves and phyllaries bearing open, thick-stalked or sessile pit-glands; each disc floret subtended by a palea, the paleae free. . . . *Holocarpus*
- 7' Leaves and phyllaries gland-bearing or not, none with pit-glands; in most spp. only the peripheral disc florets subtended by paleae, the paleae free or connate in a ring.
8. Receptacular paleae in most spp. connate and persistent; ray, or all, cypselae \pm laterally compressed and \pm arcuate (if \pm obovoid, disc florets 1–2). *Madia*
- 8' Receptacular paleae connate or free, not persistent; ray cypselae \pm obcompressed or none.
9. Ray cypselae each \pm completely invested by a subtending phyllary, the two margins of each phyllary \pm overlapping (or rays none).
10. Perennials; rays 5, corollas inconspicuous, white to purplish; pappi of 1–5 bristles or none; flowering mostly in summer and fall. *Holozonia*
- 10' Annuals; rays none or 3–27, corollas showy, variously yellow, white, or yellow/white; pappi of 2–32 bristles or subulate scales, the scales often plumose or woolly, or pappi none; flowering mostly in spring. *Layia*
- 9' Ray cypselae each only partially invested by a subtending phyllary.
11. Proximal leaves often pinnately lobed or divided; ray florets (3–)5–34+, limbs of the corollas not deeply lobed; disc florets (3–)13–60+. *Hemizonia*
- 11' Proximal leaves entire; ray florets 1–6, limbs of the corollas deeply lobed; disc florets 3–12(–25).
12. Leaves and phyllaries without tack-glands; ray cypselae beaked. *Osmadenia*
- 12' Distal leaves and phyllaries bearing tack-glands; ray cypselae not beaked. *Calycadenia*

Heliantheae—Milleriinae

Guizotia is the only genus of Milleriinae treated in *JepsMan*.

Heliantheae—Pectidinae

1. Leaves opposite, undivided, and proximally bristly-ciliate; ray florets each borne on base of a subtending phyllary; style branches short, knob-like. *Pectis*
- 1' Leaves opposite or mostly alternate, often divided or lobed, bristly-ciliate at base in few spp.; ray florets not borne on bases of subtending phyllaries; style branches linear.
2. Phyllaries free to base or nearly so.
3. Calyculus none; pappi wholly of free, coarse to fine bristles. *Porophyllum*
- 3' Calyculus of (0–)1–9 linear to deltate bractlets; pappi wholly or partially of scales (scales may be each constituted of 5–10 basally connate bristles).

- 4. Ray corollas yellow to orange. *Dyssodia*
- 4' Ray corollas white to pink or magenta. *Nicolletia*
- 2' Phyllaries connate at least $\frac{1}{4}$ their lengths (outer margins may be free to base).
- 6. Calyculus none; pappi of 2–5(–10) elements in 1 series, mostly 1–2(–5) shorter, erose or truncate plus 1–2(–5) elongate or uniaristate. . . . *Tagetes*
- 6' Calyculus present; pappi of 8–20 elements in 2 series, variously constituted, not as above.
- 7. Plants mostly less than 2 dm tall; leaves mostly linear-filiform or with linear-filiform lobes; involucre 4–6 mm high, 3–6 mm diam.; phyllaries strongly connate $\frac{2}{3}$ or more of their lengths. *Thymophylla*
- 7' Plants mostly more than 2 dm tall; leaves or lobes linear or broader; involucre 7–18 mm high, 5–12 mm diam.; phyllaries weakly connate $\frac{1}{3}$ – $\frac{2}{3}$ their lengths. *Adenophyllum*

Heliantheae—Peritylinae

- 1. Leaf blades variously lobed or entire, mostly less than 3 cm long; phyllaries 8–16 in 2–3 series, free. *Perityle*
- 1' Leaf blades triangular-hastate to narrowly deltate, not lobed, 3–12 cm long; phyllaries 15–21 in 1(–2) series, wholly or partially connate. *Pericome*

Heliantheae—Rudbeckiinae

Rudbeckia is the only genus of Rudbeckiinae treated in *JepsMan*.

III.I. Eupatorieae.

Shrubs, herbs. Leaves mostly cauline, sometimes basal or basal and cauline; mostly opposite, sometimes alternate. Phyllaries in 2–5+ series, unequal to subequal. Receptacles usually epaleate. Heads discoid. Corollas actinomorphic with short lobes—cyanic or white. Anthers ecalcarate, not tailed. Style branches usually terete to filiform, stigmatic in 2, separate lines—appendages usually 3–6+ times as long as stigmas (Figs. 27–29). Cypselae usually prismatic and 5-ribbed, sometimes 7–10-ribbed, rarely compressed. Pappi usually of bristles, sometimes bristles and scales, rarely wholly of scales or coroniform or none—bristles rarely plumose.

Key to genera treated in *JepsMan*.

- 1. Phyllaries subequal in 2–3 series, obscurely or not at all striate-nerved.
- 2. Shrubs or coarse perennials; leaves usually petiolate; florets 10–60 per head; pappi of 5–40 bristles. *Ageratina*
- 2' Annuals; leaves sessile; florets 75–125 per head; pappi of 2–6 stout bristles or narrow, aristate scales. *Trichocoronis*
- 1' Phyllaries graduated in 3–5+ series, mostly strongly striate-nerved.
- 3. Cypselae 10-ribbed; pappi of 10–50+ fine bristles, none basally dilated. . . . *Brickellia*
- 3' Cypselae 5-ribbed; pappi wholly or partly of aristate to mucous scales or basally dilated bristles.
- 4. Annuals; leaves alternate, sessile, linear; pappi of 3 aristate scales alternating with 3 mucous scales. *Malperia*
- 4' Perennials or shrubs; leaves mostly opposite, petiolate, petioles longer than

the rhombic to pentagonal blades; pappi of 12–24 aristate scales or basally dilated bristles. *Pleurocoronis*

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SIBAROPSIS (BRASSICACEAE), A NEW MONOTYPIC GENUS FROM SOUTHERN CALIFORNIA

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ABSTRACT

A recently discovered annual crucifer is the sole representative of a new genus, *Sibaropsis*. The taxon is currently known from three mountains in the Peninsular Ranges of Southern California with a disjunction of ca. 120 km between the northern and southern populations. Potential affinities with *Streptanthus* sensu lato are considered, but the true relationships of the new genus remain cryptic. *Sibaropsis* is readily distinguished from other genera by a suite of characters which includes narrowly linear cotyledons and leaves, slightly zygomorphic corollas with petal claws forming a pseudotube and laminae apically notched, three-ranked staminal configuration with the adaxial filaments partially to wholly united into a nonpetaloid staminode, oblong-ovate anthers, tardily dehiscent siliques with a beak-like style, and a disarticulating infructescence rachis. The currently known populations are restricted to sunny, low-competition, vernal saturated clay soil microhabitats, generally in association with islands of *Stipa pulchra* grassland surrounded by chaparral.

Recent floristic fieldwork in the Peninsular Ranges of Southern California has resulted in three independent discoveries of a previously undescribed annual mustard. The first known collections were ours in the spring of 1992, and were made on Elsinore Peak in the Santa Ana Mountains in southwestern Riverside County. On its discovery, it was evident that this plant was new to the local flora. After extensive literature and herbarium searches, and verification that the plant did not constitute a rare introduction, we initiated work on describing this new taxon.

In the spring of 1993, we became aware that a perplexing annual mustard had been collected that season on Poser and Viejas mountains in the southern portion of the Cuyamaca Range of San Diego County by two botanists working independently of each other. Examination of these specimens confirmed that they represented the same taxon as had been collected the previous year in the Santa Ana Mountains (Fig. 1).

While it is clear that these plants constitute a distinctive but undescribed species, determination of the proper generic placement has proven considerably more difficult. The staminal arrangement suggests affinities with *Streptanthus*, particularly members of subgenus *Euklisia*. However, other staminal, floral, and vegetative features suggest potential relationships, albeit more distant, with *Streptanthella* or the Pacific Southwestern species of *Sibara*. Taken in their

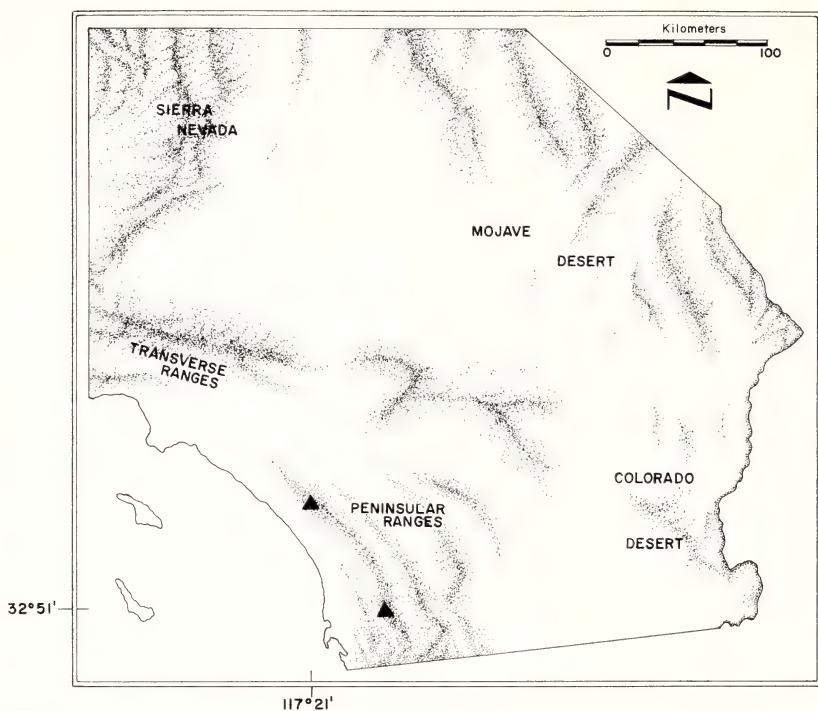


FIG. 1. Map of Southern California illustrating the disjunction between the currently known northern and southern populations of *Sibaropsis*.

entirety, however, the unique suite of morphological characters exhibited by this new species prevent its ready placement within any currently recognized genus without considerable revision and blurring of traditional generic delimitations. Consequently, pending the major revisionary work that is likely to follow in the wake of extensive molecular studies currently underway in the family (R. Price, S. O'Kane, G. Allan, and M. Porter unpublished data), we find this species best accommodated in a new genus, which we here propose.

Sibaropsis hammittii S. Boyd & T. S. Ross, gen. et sp. nov. (Fig. 2). —Type: USA, California, Riverside County, Santa Ana Mountains, Elsinore Peak area south of Lake Elsinore, on "Onion Hill," a grassy knoll about 0.5 mile southeast of Elsinore Peak on the crest of the range, north of the Main Divide Road, T6S R4W SE¼ SW¼ sec. 31 (USGS Wildomar 7.5' quadrangle), elev. 3320 ft, 1 April 1992, Boyd & Ross 6783 (holotype, RSA; isotypes, CAS, GH, MO).

Herba annua, fugax, tenella, simplex vel prope basin ramifera.

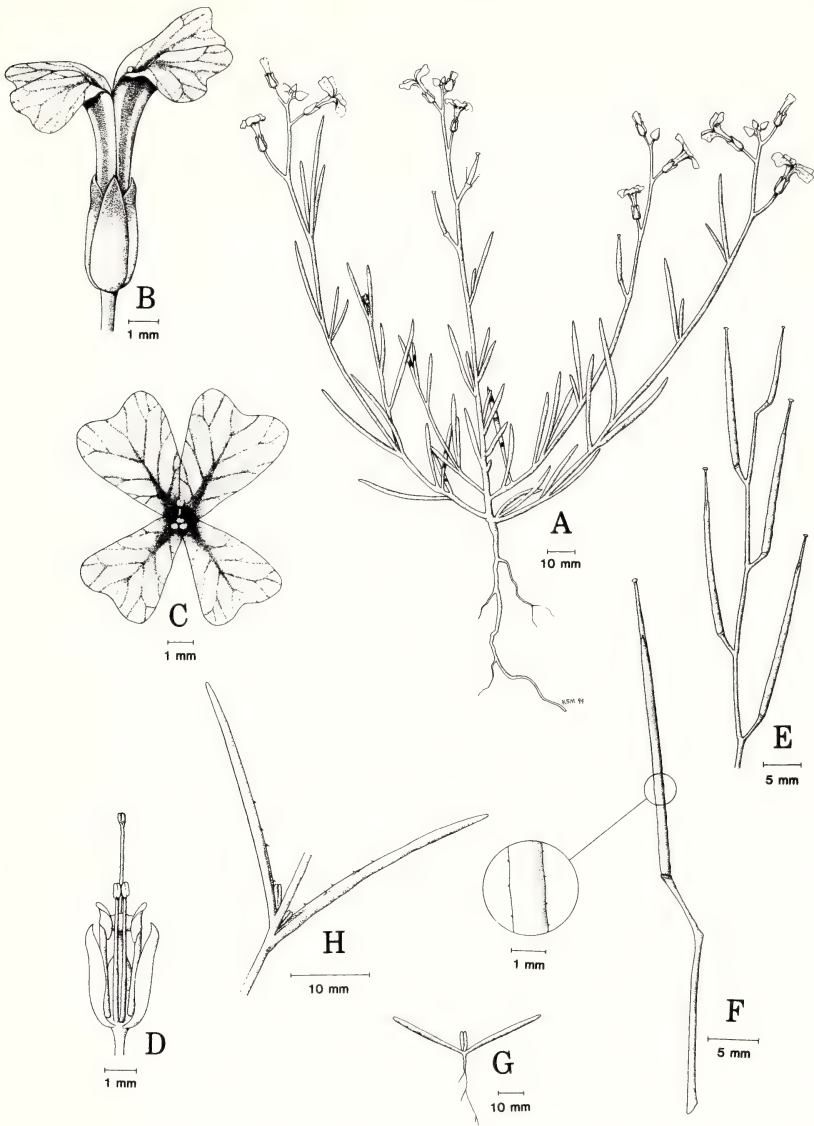


FIG. 2. *Sibaropsis hammittii* S. Boyd & T. S. Ross. A) general habit; B) lateral view of calyx and corolla with exerted pseudotube formed by the slightly imbricate margins of the petal claws; C) frontal view of corolla showing slightly zygomorphic aspect; D) abaxial view of flower (petals and abaxial sepal removed) to show three-ranked staminal configuration and dimensions of gynoecium at anthesis; E) portion of infructescence illustrating general aspect; F) disseminule consisting of a silique, its pedicel, and the subtending length of the infructescence axis (inset—microscopic trichomes present on the silique margins and beak-like style); G) cotyledons and incipient true leaves; H) lower leaves with sparse, evanescent, ciliar trichomes.

Cotyledones ad folia vera amplitudo forma et textura similes. Rami teretes ascendentes 5–15(–20) cm longi, glabri et leniter glauci. Folia anguste linearia, sessilia et non auriculata, (10–)15–30(–45) mm longa, 0.5–1.0 mm lata, subviridia et parum glauca, praeter folia infima ciliis paucis evanidis glabra, subsucculenta semiteretiaque, apicibus acutis subrotundatis stramineis. Folia plus minusve erecta vel ascendentia, subopposita necnon minime caespitosa ad primos 2–3 nodos (vero non rosulata), autem prompte alternascentia et dissita supra basin. Inflorescentia ebracteata, racemosa, floribus paucis dissitis (minus quam 10 generaliter). Internodia racemi longitudine pedicellos superantes. Pedicelli ca. 0.5 mm diametro, 2–4 mm longi sub anthesi, 3–4 mm longi ubi maturi, apicibus non amplificatis manifeste. Calyx fere cylindricus (non urceolatus). Sepala subaequalia, erecta, discreta, glabra, oblonga-lanceolata vel oblonga-ovata, ca. 3 mm longa, 0.5–1.0 mm lata, apicibus acutis et aliquando apiculatis minute, lateralibus leniter subsaccata ad bases. Corolla vulgo zygomorpha, limbo bene evoluta, et pseudotubo per unguices exsertos parum imbricatos formato. Petala imbricata (uno exteriore et quarto interiore), unguiculata-spatulata, 8.5–10.0 mm longa, expansa ad ca. 4.5–5.0 mm, apicibus laminarum 2.0–2.5 mm latis, incisuratis late non profunde, lobis deltoideis acutis rotundatis, subrosea-lavandula vel sublavandula-purpurea venationibus purpureis. Utrumque petalum adaxiale appendice basali parvula (nectarifera credimus) in basin sepali lateralis contigui insertam. Stamina in tres series inaequales disposita. Stamina fertilia 4, abaxialia et lateralibus. Filamenta glabra antherae oblongae-ovatae ferentia. Filamenta lateralibus ca. 2 mm longa antheris ca. 0.8 mm longis, et abaxialibus ca. 3 mm longa, libera vel raro connata, antheris ca. 0.5 mm longis. Filamenta adaxialibus omnino vel maximam partem connata (in specie variat etiamque in eodem individuo), ca. 4.5–5 mm longa, in staminodium subteretum non petaloideum parum exsertum modificata. Antherae staminodii vestigiales, marcidiae, ca. 0.2 mm longae, contiguae vel leniter separatae. Ovarium sub anthesi ca. 2.0 mm longum, 0.5–0.7 mm latum, stylo angustior ca. 0.2 mm longo, stigmatem discoideum ferente. Siliqua suberecta, anguste linearis, satis compressa, (15–)20–25 mm longa, 0.6–0.8 mm lata, stylo persistente tenui subrostellato (1.5–)3.0–4.5 mm longo, praeter trichomata microscopica marginales glabra, foliis positione amplitudine ambitu et colori similis, maxime tarde dehiscens. Infructescentia ubi matura in segmenta frangens, unumquidque siliqua pedicello et parte infructescentiae rhachidis capientia. Sementes 1-seriata, non mucosa, oblonga, compressa, plus minusve truncata obtusiuscule ad hilum, rotundata et non nisi microscopicaliter alata ad extremum distale, paginis minute striatis vel grosse scalpratis. Cotyledones incumbentes.

Delicate, short-lived, cool season *annual*, freely branched at and

near the base. *Cotyledons* narrowly linear, attaining similar size, shape, and texture to the true leaves. *Axillary buds* of the cotyledons occasionally developing (in the absence of apical damage), but generally later than those of the lowermost true leaves. *Branches* terete, ascending, 5–15(–20) cm long, glabrous and slightly glaucous, light green but often with a faint purplish suffusion or mottling, especially above. *Leaves* narrowly linear, sessile and lacking auricles, (10–) 15–30(–45) mm long, 0.5–1.0 mm wide, light green and slightly glaucous, glabrous except for a few scattered, evanescent cilia on those of the lowest nodes (poorly developed or absent in depauperate plants); somewhat fleshy and semi-terete, the adaxial surface slightly flattened, the abaxial surface rounded; apex acute, slightly rounded, yellowish. True basal rosette lacking, the cotyledons and leaves of the first two to three nodes initially tufted prior to elongation of the internodes. Leaves \pm erect-ascending, opposite at the first 1–2(–3) nodes of the main axis and lowermost branches, becoming alternate above, uncongested. *Inflorescence* ebracteate, loosely racemose, relatively few flowered (mostly fewer than 10). Flower buds initially crowded, raceme internodes elongating at and after anthesis, becoming longer than the pedicels. *Pedicels* slender, ca. 0.5 mm diameter, 2–4 mm long at anthesis, 3–4 mm in fruit, not markedly expanded at their apices. *Calyx* tubular, glabrous. The four *sepals* subequal, erect, free to their bases, purplish to greenish purple with paler bases and narrow whitish bands on their margins, oblong-lanceolate to oblong-ovate, ca. 3 mm long, 0.5–1.0 mm wide; the apex acute, sometimes minutely apiculate, the lateral sepals only very slightly saccate at their bases. *Corolla* slightly zygomorphic with a well-developed limb and a pseudotube formed by the slightly imbricate margins of the well-exserted petal claws. The four *petals* unguiculate-spatulate, 8.5–10.0 mm long, spreading at ca. 4.5–5.0 mm; the apex 2.0–2.5 mm wide, shallowly and broadly notched, the deltoid lobes acute, rounded; light purplish-lavender or pinkish-lavender with darker purplish veins, aging to a more saturated purplish prior to withering. Upper petals with a small basal appendage (presumably nectariferous) directed into the base of the adjacent lateral sepal lobe. *Stamens* arranged in three unequal series. Fertile stamens 4, lateral and abaxial in position, the filaments glabrous, mostly pale yellowish-white except at the tip where purplish, bearing oblong-ovate anthers; the lateral pair of filaments ca. 2 mm long, with stamens ca. 0.8 mm long; the abaxial pair longer and closely juxtaposed but usually free (uncommonly connate), ca. 3 mm long, with anthers ca. 0.5 mm. Abaxial stamens maturing before the lateral. Pollen pale yellow. Filaments of adaxial stamen pair partly to wholly connate, ca. 4.5–5.0 mm long, modified into a *staminode* slightly exserted from the mouth of the corolla; upper $\frac{1}{2}$ to $\frac{2}{3}$ dark purple, paler below. Sterile anther sacs of the staminode vestigial,

reduced to whitish, wrinkled structures ca. 0.2 mm long, mostly closely placed, but occasionally slightly separated on the bifurcate staminode tip; bifurcation 0–2.0 mm deep, variable even within individuals. *Ovary* at anthesis oblong, ca. 2.0 mm long, 0.5–0.7 mm wide; style narrower, ca. 0.2 mm long, bearing an unlobed, discoid stigma which slightly exceeds the style diameter. *Fruit* a tardily dehiscent silique, suberect, narrowly linear and somewhat flattened parallel to the septum, (15–)20–25 mm long, 0.6–0.8 mm wide, with a slender, persistent, moderately beak-like style (1.5–)3.0–4.5 mm long; glabrous except for scattered, clear, simple microscopic hairs along the lateral sutures and stylar beak; similar to the leaves in orientation, size, shape, and color (when immature). At maturity, leaves wither and fall away leaving the branch architecture and ascending siliques, which dry to a light tan or chestnut brown color. *Infructescence* ultimately disarticulating at abscission zones along the central axis, just above each pedicel, the functional dispersal unit then comprising a silique with its pedicel and a length of the infructescence axis. The exception to this pattern is the lowest silique of each flowering branch, which remains attached to the dried plant base. *Seeds* uniseriate, non-musculaginous, oblong, ca. 1.2 mm long, 0.5 mm wide, reddish-brown to dark olive-brown with minutely striate or chiseled surfaces, laterally flattened, \pm truncate at the pylar end (sometimes obliquely so), rounded and only microscopically winged distally (Fig. 3). Cotyledons incumbent. Chromosomes: $2n=28$.

Paratypes. USA, California, Riverside County, Santa Ana Mountains, clay soil areas on Elsinore Peak, T6S R4W SW $\frac{1}{4}$ sec. 31 (USGS Wildomar 7.5' quadrangle), elev. 3320–3360 ft, 31 March 1992, Boyd & Ross 6771, (RSA, F, K, MEXU, NY, SD, UC, UCR, US); San Diego County, Viejas Mountain, on Forest Service land ca. 1 mile northeast of intersection of Viejas Grade and Willow Road (directly above 19520 Viejas Grade), 25 March 1993, Hirshberg 197 (SD); Poser Mountain, 0.7 mile east of intersection of Red Oak Road and Viejas Grade, east side of road, 6 April 1993, Reiser s.n. (SD).

Etymology. The generic name (*Sibara*, anagram of *Arabis*, coined by E. L. Greene; and *opsis* [Greek], resembling in appearance) alludes to the general floral similarity of the taxon to the *Sibara* species of the Pacific Southwest. The specific epithet honors our colleague and esteemed friend, Mike Hammitt (1957–1991), an enthusiastic Southern California naturalist whose untimely death cut short a very promising life of discovery. Because common names are frequently considered desirable for the lay-person, we propose “Hammitt’s clay-cress” as the vernacular for this rare species.

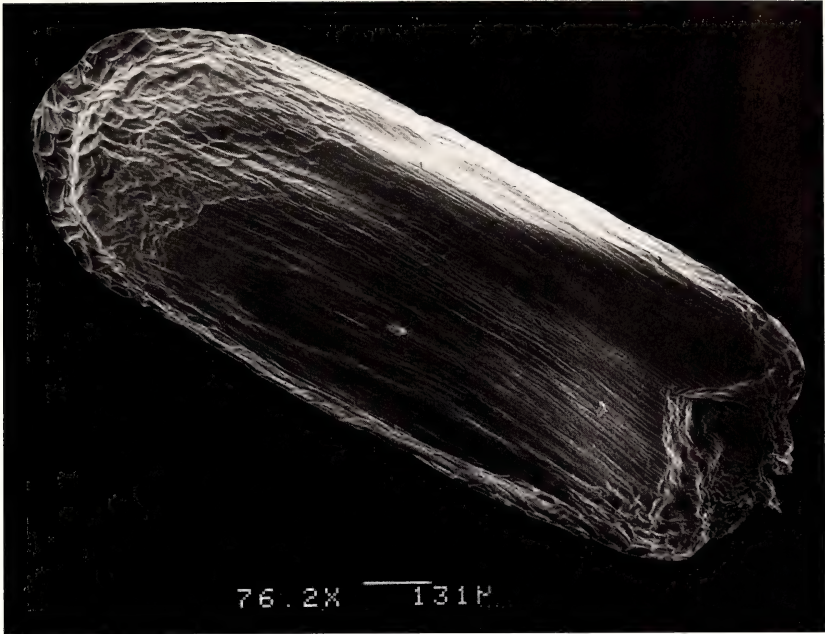


FIG. 3. Scanning electron micrograph of a representative seed of *Sibaropsis hammitii* illustrating the striate or partially chiselled seed coat pattern, and the vestigial, microscopic wing at the distal end.

POTENTIAL TAXONOMIC AFFINITIES

The Brassicaceae, while one of the better marked and natural flowering plant families, is notable for the considerable difficulties encountered in delimiting its component genera (Al-Shehbaz 1973). It is widely accepted that generic boundaries in the family are often arbitrarily drawn, confounding efforts to understand natural lineages and intergeneric relationships (Al-Shehbaz 1984). Examples in which two or more genera exhibit morphological overlap are so numerous in the family as to be almost the rule, rather than the exception (Rollins 1982). As a result, the family is characterized by a remarkably high percentage of oligotypic genera: 40% monotypic, with an additional 33% represented by 5 or fewer species (Al-Shehbaz 1984).

Against this backdrop of often tenuous supraspecific entities, determining the appropriate generic placement for *Sibaropsis hammitii* has proven a difficult task. Shortly after its original discovery in 1992, during which time we sought to establish whether the species was native or introduced, we investigated potential affinities of *Sibaropsis* with several genera primarily from North America, Eurasia, and northern Africa. Based on the literature, various genera showed

potential morphological similarities, among them the Mediterranean *Moricandia*, *Malcolmia*, *Chorispora*, and the Central Asian *Dontostemon*. Surveys of the known species in these and other genera consistently resulted in dead-ends, and incrementally excluded the possibility that the new taxon was a rare introduction from another arid region of the world. After confirming its native status to the degree possible, we began to focus more closely on its potential relationships with other North American taxa. The unusual staminal configuration in *Sibaropsis*, if made the exclusive focal point of taxonomic comparison, would suggest potential generic placement in the genus *Streptanthus*.

This genus, as treated by Rollins (1993), consists of 33 species occurring in the western and southwestern United States as well as northern Mexico. It is taxonomically associated with several other genera whose true relationships remain problematic. *Caulanthus*, a western North American genus of ca. 13–16 species, and *Stanfordia*, a monotypic genus of south-central and western California (Rollins 1993), have been treated tentatively by Rodman et al. (1981) in an expanded concept of *Streptanthus*. Under this broader circumscription, which we will discuss here as “*Streptanthus sensu lato*,” the genus consists of about 50 species parceled among five subgenera, and includes annual, biennial, and perennial herbs (Rodman et al. 1981; Al-Shehbaz 1985). Its greatest species diversity is found in California, where many species are edaphic endemics, particularly on serpentine or other ultramafic substrates (Buck et al. 1993; Rollins 1993). Traditionally placed within the tribe Thelypodieae, the genus is united by a diagnostic floral morphology which includes zygomorphic calyx and/or corolla, and three-ranked stamens, the longest set often (but not always) with fused filaments and reduced anthers (Schulz 1936; Rollins 1993).

The slightly zygomorphic corolla and three-ranked staminal configuration of *Sibaropsis*, particularly the modification of the longest set into a staminode, provides the most compelling argument for inferring a close relationship with *Streptanthus*, in which this staminal configuration is otherwise considered unique. If *Sibaropsis* were treated as a *Streptanthus*, its possession of a staminode would likely require that it be placed within subg. *Euklisia*, a group which includes annuals and biennials and is distributed from central cis-montane California northward to extreme southwestern Oregon (Hoffman 1952; Buck et al. 1993). Alternately, its anomalous characters might suggest its treatment as a monotypic subgenus within *Streptanthus*.

There are, however, some important differences between *Streptanthus* and *Sibaropsis* with respect to the shared staminodial structure and general anther morphology. In *Streptanthus* subg. *Euklisia*, the fused filaments are relatively broad and petaloid and, in most

species, the vascular traces of the filaments are readily visible and clearly separate. In *Sibaropsis*, the staminodial filament is narrow, more or less terete, and without readily visible paired vascular traces. In *Streptanthus*, the fertile anthers, as well as the reduced anthers of the staminode, are essentially the same shape: linear-sagittate with an acute apex. In *Sibaropsis*, however, the fertile anthers are oblong-ovate with a rounded apex, and the reduced anther sacs of the staminode are small and shriveled, retaining no particular shape.

The flowers of *Streptanthus* may be zygomorphic or actinomorphic. Unlike the tubular, essentially actinomorphic calyx of *Sibaropsis*, with its small, erect lobes of fairly uniform size and shape, the calyces of most *Streptanthus* species are relatively large, and frequently inflated or flask-shaped. This is particularly true of those in the subg. *Euklisia*, reaching an extreme in *S. polygaloides* A. Gray. Petal morphology, as with other characters, varies considerably within *Streptanthus* sensu lato. In the subg. *Euklisia* the petals typically have a broad claw and a narrow, crisped blade without an apical notch. These are in contrast to the petals of *Sibaropsis*, which have a narrow claw that broadens rather abruptly into the apically notched, expanded lamina.

Another morphological character worth considering in *Sibaropsis* is the elongate, persistent, beak-like style. Although no ovarian tissue occurs within it, and it can by no means be considered a true "beak" as the term is generally applied in the crucifers, its presence and form clearly distinguish the taxon from *Streptanthus* sensu lato, in which the styles tend to be short and blunt, the stigmas in a few taxa being nearly sessile.

Seed morphology varies considerably within *Streptanthus* sensu lato, and the gross external features and size of *Sibaropsis* seeds would not necessarily be excluded from the range of variation evident in *Streptanthus* subg. *Euklisia*. It is of interest, nevertheless, to consider cotyledon position here. Embryo configuration has often been given consideration in the Brassicaceae due to its uniformity in many groups. Unfortunately, it may also be variable within genera, leading some students of the family to discount its value as a taxonomic character (Murley 1951). Within *Streptanthus* sensu lato, where cotyledon position is somewhat variable, it may be accumbent or obliquely accumbent (*Streptanthus* sensu stricto, *Caulanthus* pro parte), obliquely incumbent (*Caulanthus* pro parte), or coiled (*Stanfordia*) (Rollins 1993). All species of *Streptanthus* subg. *Euklisia*, however, have seeds with accumbent cotyledons while those of *Sibaropsis* are incumbent.

Leaf morphology in *Streptanthus* is highly variable and may range from broadly ovate or obovate to linear-lanceolate. Likewise, the leaves may be petiolate or sessile (usually above), and may or may not be auriculate at their bases. The lowest leaves may be clustered

or not, but there is a notable tendency toward dimorphism between the basal and cauline leaves which is often quite dramatic. As with most crucifers, there is also a great morphological difference between the cotyledons and the true leaves. In contrast, there is remarkable uniformity in the leaves of *Sibaropsis*, from the narrowly-linear cotyledons, to the first true leaves, to the uppermost leaves subtending the racemes. No species of *Streptanthus* has leaves remotely approaching the narrowly linear, semiterete leaves of *Sibaropsis*.

In addition to these differences, none of the species of *Streptanthus* is recorded as having linear cotyledons. Certainly, none of the species has tardily dehiscent siliques, or disarticulating infructescence axes.

As has been noted, a putative alliance of *Sibaropsis* with *Streptanthus* rests very heavily on shared aspects of the highly modified staminal configuration, but does so to the exclusion of other important morphological characters. We have preferred to assess the organism in toto, and have not abandoned the possibility that such a morphological trait could have originated independently of *Streptanthus* through similar selective pressures of pollinators.

While this staminal arrangement is unusual in the family as a whole, and the particular combination has, until now, been considered unique to *Streptanthus*, the component elements of this character on an individual basis are neither unique to, nor universally present within the genus (Rollins 1993). For example, three-ranked stamens are also reported for the New World genus *Streptanthella* and the Old World *Camelina* (Schulz 1936; Rollins 1993), while fusion of the filaments of the adaxial paired stamens is found in both Old World genera (*Blenodia*, *Dontostemon*, *Euzomodendron*, *Orychophragmus*) and New (*Glaucocarpum* and *Thelypodium*) (Schulz 1936).

There are, of course, additional genera—and morphological characters—that could be brought into this discussion of potential affinities. In our assessment of *Sibaropsis* and its potential alliances, we have remained cognizant of the traditional weight placed on floral structure and fruit morphology, but have also tried to balance these with other morphological traits that equally characterize the taxon, and which may also be subject to adaptive pressures over geologic time, or random, advantageous mutations. With its overall suite of characters considered, *Sibaropsis* appears to be allied with such genera as *Streptanthus*, *Caulanthus*, and *Streptanthella* in the tribe Thelypodieae, as well as the Pacific Southwestern species of *Sibara*, which we feel are misplaced in their traditional alliance with the Arabideae.

In this context, the somatic chromosome count obtained for *Sibaropsis hammittii* is worth commenting on. The material counted

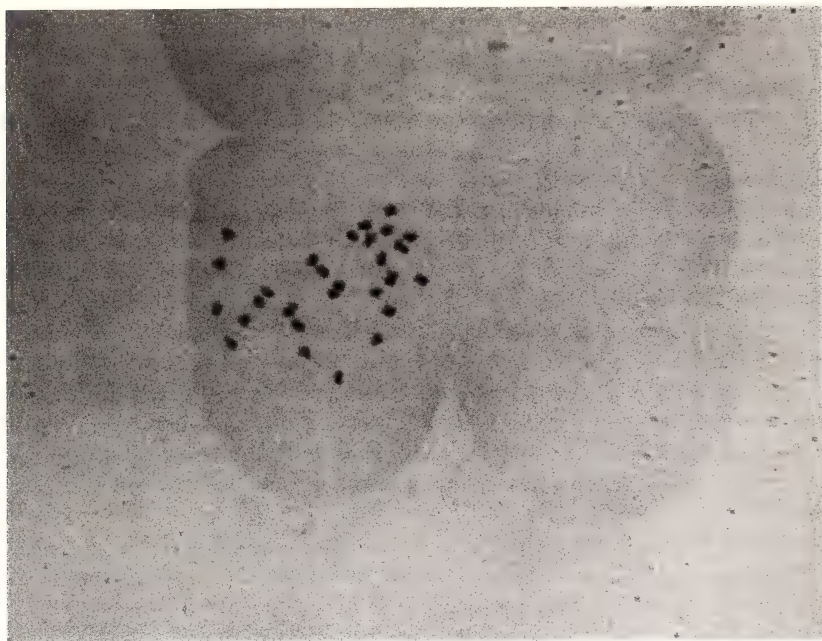


FIG. 4. Photograph of a root-tip chromosome preparation of *Sibaropsis hammittii* showing a somatic count of $2n=28$ [Cultivated voucher: S. Boyd 8203A (RSA)].

was derived from seeds of cultivated F_2 plants originating at the type locality. Root tip squashes were prepared following the protocol of Li (1982) and indicated a count of $2n=28$ (Fig. 4). Although this number is somewhat unusual in the family, it is typical of the monotypic *Streptanthella* and *Stanfordia*, most species in the genera *Caulanthus* and *Streptanthus*, as well as *Sibara angelorum* and *S. laxa* (counts for *S. brandegeana* and *S. filifolia* are not available) (R. Price personal communication; Rollins 1993). This may tend to suggest a close relationship among these lineages. However, extensive chromosomal studies have not yet been conducted throughout the Thelypodieae and counts are still unavailable for a majority of the taxa. Such wide gaps in the data preclude a clearer assessment of the overall chromosomal patterns in the tribe.

Having already addressed some of the attributes of *Streptanthus* *sensu lato*, discussion of the less obvious potential relationships to *Sibara* and *Streptanthella* is perhaps warranted here.

Sibara is a small North American genus traditionally considered most closely related to *Arabis*, in the tribe Arabideae (Rollins 1947, 1982, 1993; Al-Shehbaz 1988). Within *Sibara*, we informally recognize three phytogeographically and morphologically distinct assemblages which we refer to here as "the Virginica group" (4 spe-

cies), "the Deserti group" (2 species), and "the Angelorum group" (4 species). The first two groups we believe to represent more distant lineages and they will not be considered further here. The Angelorum group, however, approximates the generic concept established by E. L. Greene (1896) and is a seemingly more natural Pacific Southwestern assemblage of annuals comprised of *S. angelorum* (S. Watson) Greene, considered the type species by Greene [incl. *S. pectinata* (Greene) Greene]; *S. laxa* (S. Watson) Greene; *S. brandegeana* (Rose) Greene; and *S. filifolia* (Greene) Greene. The former three occur in the central deserts of Baja California, Mexico, although *S. angelorum* ranges farther northeast into Sonora state (Wiggins 1980). The last, *S. filifolia*, is an exceedingly rare insular endemic only known extant on the southerly extreme of San Clemente Island (Rollins 1947, 1993; Beauchamp 1987; Skinner & Pavlik 1994). It is this third suite of species (the Angelorum group) that we refer to as *Sibara* sensu stricto and which we compare to the new taxon.

Sibara sensu stricto possesses a few characters worth considering in relation to *Sibaropsis*, although there are also important morphological differences. Foremost in similarity are such characters as anther shape, seeds, and gross features of the leaves, calyx, and petals.

Surprisingly little information has been published on anther morphology of *Sibara* sensu stricto; however, it is apparent that Greene's (1896) characterization of the anthers as "linear-sagittate" is incomplete. Our examination of numerous dried specimens of *Sibara* housed at RSA-POM as well as fixed flowering material confirms the report by Al-Shehbaz (1988) that the anthers of *Sibara* may be oblong to ovate, as well as linear-sagittate. In relative size and shape, the fertile anthers of *Sibaropsis* closely resemble the anthers of *Sibara angelorum*.

In terms of seed morphology, both *Sibara* and *Sibaropsis* have seeds that are oblong and essentially wingless. In *Sibara*, cotyledon position is variable and may be accumbent (*S. angelorum*), or incumbent (*S. brandegeana* and *S. laxa*; obliquely so in *S. filifolia*) as are those of *Sibaropsis*.

As for more plastic features, the leaves of *Sibara* are glaucous and somewhat fleshy, and are pinnatifid or pectinate with linear rachises and narrowly-linear lobes. In depauperate plants there is a tendency toward reduction in the number of lobes and the upper cauline leaves are not uncommonly sessile, entire, and narrowly linear. Were the narrowly-linear leaves of *Sibaropsis* derived from a progenitor of similar morphology, one might hypothesize the fixation of such a character in a diminutive, short-lived species. Such adaptive changes in vegetative features are likely as easily attained

and genetically fixed as would be similarly dramatic changes in floral morphology that result in a new pollination syndrome.

The calyx of *Sibaropsis*, with its small, erect lobes of uniform size and shape, is essentially actinomorphic and quite similar to that of *Sibara*. In both genera, the lateral sepals are only very slightly saccate, and the calyx is entirely glabrous (Rollins 1993). Although there do appear to be general morphological trends within most cruciferous genera, little is known, unfortunately, of the selective pressures that may act on calyx morphology.

Also of great similarity, but undoubtedly subject to tremendous selective pressures of pollinators, are the size, shape, and coloration of the petals in both *Sibaropsis* and *Sibara*. Both occur in \pm lavender shades with darker veins, and have narrow claws with broad, \pm plane laminae which are apically notched. While such petals are relatively uncommon among crucifers in western North America, the characters are present in other quite unrelated genera, such as *Malcolmia* and *Leavenworthia*, and have clearly arisen on multiple occasions (Rollins 1993). An important structural difference between *Sibaropsis* and *Sibara* is that the corolla of the former bears a distinctive pseudotube exerted above the calyx, while the petals of the latter are spread at the summit of the sepals.

Among the more notable dissimilarities are the linear cotyledons of *Sibaropsis*, which gradually expand in size until they quite resemble the narrowly-linear true leaves. In contrast, the cotyledons of *Sibara* tend to be broadly ovate-elliptic and never approximate the morphology or size of the true leaves.

Additionally, the mature silique valves of *Sibara* are readily dehiscent, as is common in most crucifers, while the tardily dehiscent siliques of *Sibaropsis* apparently open only with age or weathering. In *Sibaropsis*, the disarticulation of the infructescence axis at abscission zones differs not only from *Sibara*, but appears to be unknown in any other crucifer. Perhaps the most similar case occurs in the genus *Warea* (Thelypodieae), with four species in the southeastern United States, in which the infructescence axis remains intact but the fruiting pedicels often abscise from the axis (Rollins 1993).

An important character that obviously differentiates *Sibaropsis* from *Sibara* is the staminal configuration. In *Sibara*, the stamens are consistently two-ranked (tetradynamous) with all anther sacs bearing fertile pollen, while the three-ranked staminal configuration in *Sibaropsis*, with the additional fusion of the adaxial pair into a staminode (Fig. 2D), presents an unusual architecture with unknown advantages but which is presumably associated with pollinator attraction and/or orientation. As with petal coloration and morphology, stamen length and connation are likely subject to similar selective pressures over geologic time, and are limited only by the genetic potential of the progenitor.

Another genus which does possess three-ranked stamens, but which otherwise might not be readily thought of as a potential ally to *Sibaropsis*, is *Streptanthella*. This is a somewhat variable but monotypic genus widely distributed in xeric portions of the American West, from Washington, Montana, and Idaho southward to New Mexico, Baja California, and Sonora, Mexico (Munz and Keck 1959; Rollins 1993). It is a glaucous, narrow-leaved annual of sandy to gravelly soils, and is particularly noted for its siliques with a beak-like, indehiscent tip ca. 3–4 mm long, for which it has received the epithet *S. longirostris* (S. Watson) Rydberg.

This beak-like silique tip is similar in form and dimension to that of *Sibaropsis*, and the indehiscent character of the distal portion of the fruit might lead one to hypothesize a relationship due to the intermediacy of the silique valve dehiscence. The cotyledons of *Streptanthella*, like *Sibaropsis*, are incumbent, although they may often be so in an oblique manner (Rollins 1993). In addition, *Streptanthella* is apparently unusual in the Thelypodieae in possessing linear cotyledons (R. Buck personal communication). The leaves of *Streptanthella* tend to be fairly narrow and with a definite bifacial lamina, but may be divided into linear lobes or be simple and \pm linear above. As mentioned in the discussion of *Sibara*, one might envision the fixation of such a reduced, linear leaf morphology in *Sibaropsis* if it were potentially derived from a progenitor with similarly divided leaves. In the case of *Streptanthella*, however, in which the cotyledons themselves are linear, one might even hypothesize the retention of paedomorphic traits if additional lines of evidence suggested such a derivation.

Streptanthella, on the other hand, differs in a sufficient number of morphological traits that only a loose alliance can be postulated. While the calyx is similar to that of *Sibaropsis*, the lateral sepals are more distinctly saccate basally; the stamens, though three-ranked, are all fertile with free filaments, and bear linear-sagittate anthers; the petals are narrowly spatulate without an apical notch, not much surpassing the sepals, and range from white to pale yellow (often with purplish veins); and the seeds bear a narrow wing along their margins (Rollins 1993).

While it is clear that the morphological similarities between *Sibara* sensu stricto, *Streptanthella*, and *Sibaropsis* do not necessarily intimate a direct relationship, we believe that they are sufficiently enticing to merit careful exploration at the molecular level within the context of a broad-based phylogenetic study. Unfortunately, the Thelypodieae in western North America appear to be the result of a rapid and explosive radiation which obfuscates the true relationships of its parts and renders difficult an objective taxonomic scheme based on gross morphology.

Our efforts have focused largely on proper generic placement for

the new species and, failing that, on its possible generic relationships. Based on current knowledge, however, we cannot yet surmise what the sister taxon to *Sibaropsis hammittii* may be. It is clear that an understanding of relationships in the Brassicaceae is hampered by both the artificiality of many genera, and the dogmatic weighting of certain characters to the exclusion of others. Future systematic endeavor among the mustards will benefit from a more holistic approach to the species, micromorphological studies, and the careful use of molecular techniques to divest the taxa of similarities resulting from convergence.

In the absence of a broad-based, highly inclusive molecular study of the Brassicaceae, we find it most appropriate to propose generic standing for this new species. The unique suite of morphological characters found in *Sibaropsis*, specifically the narrowly linear cotyledons and leaves; zygomorphic, pseudotubular corolla; three-ranked stamens with a subterete staminode; oblong-ovate anthers; tardily dehiscent fruit with a beak-like style; and disarticulating infructescence rachis; readily set the taxon apart from any other currently recognized crucifer genera.

HABITAT, LIFE HISTORY, AND CONSERVATION CONSIDERATIONS

At the original discovery site on Elsinore Peak, *Sibaropsis* occurs on clay soils in grassland vegetation dominated by *Stipa pulchra* A. Hitchc. in association with a rich assemblage of annual and perennial herbs. These areas of *Stipa* grassland are fairly broad, with the clay soil habitat present as discrete, island-like patches within a surrounding matrix of taller-statured chaparral vegetation. This chaparral formation is largely dominated by *Adenostoma fasciculatum* Hook. & Arn. and tends to occur on coarser soils which are locally derived from granitics. On Elsinore Peak, which we refer to as the northern population center, clay is derived primarily from local weathering of Pleistocene basalt outcrops, and to a lesser extent, Eocene marine sediments (Rogers 1965). These soils are mapped locally as the Bosanko series (Knecht 1971). Species commonly associated with *Sibaropsis hammittii* in this habitat include *Sisyrinchium bellum* S. Watson, *Lomatium dasycarpum* (Torrey & A. Gray) J. Coulter & Rose, *Dichelostemma pulchellum* (Salisb.) Heller, *Sanicula bipinnatifida* Hook., *Stipa lepida* A. Hitchc., *Allium haematochiton* S. Watson, *Fritillaria biflora* Lindley, and *Corethrogyne filaginifolia* (Hook. & Arn.) Nutt.

On Poser and Viejas mountains, *Sibaropsis* is also associated with a *Stipa pulchra*-dominated vegetation type on disjunct islands of clay soil surrounded by *Adenostoma* chaparral. However, both the derivation of the clay and the physiognomy of the vegetation differ from those at Elsinore Peak. At this southern population center, clay

is developed on colluvial deposits of basic intrusive gabbro (Cuyamaca Gabbro or San Marcos Gabbro) of Mesozoic age (Strand 1962). These soils are mapped as Auld clay (Bowman 1973). Although the habitat is relatively open and includes the associated species mentioned above, there is also a greater abundance of suffrutescent species and low shrubs, most notably *Salvia apiana* Jepson, *Eriogonum fasciculatum* Benth., *Eriophyllum confertiflorum* (DC.) A. Gray, *Gutierrezia* sp., and *Artemisia californica* Less. These tend to be scattered about the grassland and are generally more compact than they usually appear in other habitats.

At both sites, however, *Sibaropsis* is not found throughout the habitat, nor is it characteristically abundant. Instead, it is limited to the most mesic microsites on fairly open soil in which the clay substrate remains saturated with water throughout the winter and early spring. Populations of *Sibaropsis* are relatively small in both total number of individuals present and in areal extent. Generally, the species may be found where it receives direct sun during the day, and where water runs in thin sheets or rivulets, or seeps to the surface, following the seasonal rains. Apparently critical to its establishment and successful growth is a constant supply of moisture around the root system from germination through maturity, coupled with low competition. At Elsinore Peak, for example, we have observed small, sporadic populations on clay soil along the course of a small surface rivulet, but at the margin of the clay outcrop where it graded into granitic soils with better surface and subsurface drainage, the *Sibaropsis* plants were absent. The same observations were made at Poser and Viejas mountains where the fine clay soils graded into coarser soils. The fact that *Sibaropsis* is apparently limited to distribution on clay soils is probably a result of the physical properties of the soil (expansive with high water-holding capacity), rather than to a physiological requirement for, or tolerance of, a particular element or micronutrient in the substrate. We have been able to successfully cultivate the species on substrates other than clay, provided the substrate did not dry out until flowering and seed set were complete.

Given the apparently narrow parameters of the microhabitat successfully occupied by *Sibaropsis*, the seed dispersal mode seems very well-suited to maintaining the species within an area suitable for establishment and maturation. A fairly dynamic silique dehiscence would potentially waste a considerable number of seeds by disseminating them into the adjacent chaparral. In contrast, the tardily dehiscent siliques, and disarticulating infructescences, allow deposition of the seeds largely in the immediate vicinity of the parent plant. The actual disarticulation of the infructescence is probably accomplished both by weathering effects and by mechanical damage (wind, animals wandering across the grasslands, etc.). At maturity,

the siliques may generally only be opened with considerable physical manipulation. In cultivated plants, siliques have been observed to remain intact throughout the summer and autumn, splitting open only with the soaking of the first winter rains. It is possible, however, that in the natural habitat some of the silique valves may open over a shorter period of time with the effects of day-time heat and night-time dews.

While the dispersal mode of *Sibaropsis* is appropriate for maintaining it within its narrow habitat, that same dispersal mode makes the major disjunction between the northern and southern population centers quite perplexing. The populations at Elsinore Peak are separated from those of Poser and Viejas mountains by a linear distance of over 120 km. Aside from the microhabitat parameters within the *Stipa* grasslands, habitat correlations between the two population centers are more difficult to establish. Based on the few populations known, one might surmise that the species is restricted to the Peninsular Ranges of austral California. Other extrapolations can only be of the coarsest kind at this point in time.

At the currently known localities, *Sibaropsis hammittii* is found at moderate elevations in areas with direct access to the influx of marine air. This cool, moisture-laden air is particularly prevalent during the winter and spring and plays an important role in moderating inland climate. On Elsinore Peak, the *Sibaropsis* populations occur between 975 m and 1067 m, approximately 34 km inland from the coast. The elevational range on Viejas and Poser mountains is somewhat broader, 730 m to 975 m, with populations located 43 to 49 km inland from the ocean.

The Peninsular Ranges also harbor many other islands of Pleistocene basalt and/or basic intrusive gabbro between both population centers as well as southward. Many of these outcrops may bear potential habitat that ought to be surveyed for the presence of *Sibaropsis*. In all likelihood, future, appropriately-timed surveys of these habitats will reveal the presence of additional populations. Attention should particularly be given to areas under coastal influence and at elevations above 500 m. Among the localities meriting focused surveys are the higher gabbro and metavolcanic peaks of San Diego County and adjacent northwestern Baja California, Mexico (e.g., Otay, Tecate, San Miguel, Jamul, Cerro Bola, Cuyamaca, McGinty, Guatay, Iron, and Agua Tibia), as well as the basaltic Santa Rosa Plateau region of the Santa Ana Mountains.

The prospects for long-term preservation of the known populations of *Sibaropsis hammittii* seem encouraging. Both the northern and southern population centers are situated primarily on public lands administered by the Cleveland National Forest, although some stands (or subpopulations) occur on privately-held and Indian Reservation lands.

In both areas, *Sibaropsis* is closely associated with other sensitive plant species which are already receiving considerable management attention (*Allium munzii* [Ownbey ex Traub] D. McNeal at Elsinore Peak; *Acanthomintha ilicifolia* [A. Gray] A. Gray at Viejas and Poser mountains). The significance of the *Sibaropsis* populations should serve to increase attention toward the conservation needs of the sites, thereby increasing overall protection of these habitats and all taxa present.

The benefits of public land ownership to *Sibaropsis*, especially existing compatible resource management activities, are tempered by the fact that both population centers occur near the edge of the National Forest, adjacent to areas undergoing rapid urbanization. External, anthropogenically mediated threats are to be expected and may prove the most intractable management problem. In particular, increased fire frequency (as well as post-fire seeding of invasive non-native species), trampling, habitat damage by off-road vehicles (a particular concern at Elsinore Peak), and the concomitant invasion of the clay soil habitat by aggressive alien weeds, could each have serious negative effects on *Sibaropsis hammittii*. Among the potentially problematic alien species are *Avena barbata* Brot., *A. fatua* L., *Bromus hordeaceus* L., *B. madritensis* L. ssp. *rubens* (L.) Husnot, *Schismus barbatus* (L.) Thell., *Erodium cicutarium* (L.) L'Her., *E. botrys* (Cav.) Bertol., *E. brachycarpum* (Godron) Thell., *Centaurea melitensis* L., and *Brassica geniculata* (Desf.) J. Ball. These species are already present to varying degrees at sites occupied by *Sibaropsis*.

While formal legal protection for *Sibaropsis hammittii* (i.e., listing under state or federal Endangered Species Acts) seems unnecessary at the present time, future action would be warranted if downward trends in population size or vigor are noted.

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DUDLEYA GNOMA (CRASSULACEAE): A NEW, RARE SPECIES FROM SANTA ROSA ISLAND

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ABSTRACT

Dudleya gnoma is endemic to a single California island. It appears most similar to a Channel Islands endemic, *D. greenii*, and the more widespread *D. caespitosa*. It differs from *D. greenii* and *D. caespitosa* chiefly by its smaller size, smaller rosettes, shorter leaves, narrower peduncles, shorter and less-branched inflorescences, earlier flowering season, and habitat. Glaucous forms of *D. candelabrum* Rose have now been found on two of the northern Channel Islands, but that species is not easily confused with *D. gnoma*. *Dudleya gnoma* is placed in subg. *Dudleya* based on its evergreen leaves with broad bases, broad rather than terete leaves, and erect or fairly erect petals.

The name *Dudleya greenii* forma *nana* was originally proposed in a dissertation (Moran 1951) and was applied to a population of small plants found only on East Point, Santa Rosa Island. The plants had been discovered the previous year by Reid Moran. Though other aspects of the dissertation were published (e.g., Moran and Uhl 1952; Uhl and Moran 1953), the name itself was never validly published. Moran decided not to formally recognize the taxon. His reluctance was due at least in part to unresolved taxonomic problems in *D. greenii* and the *D. caespitosa* complex and also due to the presence of *D. greenii* on the same island (Moran 1951 and Moran, personal communication April 1994).

By 1993, "forma *nana*" was still only known from Moran's original collection site on infrequently visited East Point. In May 1993, I examined many dudleyas on Santa Rosa Island with the cooperation of the National Park Service. Sarah Chaney (of the NPS) and I found two additional colonies of "forma *nana*", not realizing that those two colonies had been discovered shortly before by Steve Junak of the Santa Barbara Botanic Garden.

Shortly afterwards, Thomson (1993) described a new species based on the Santa Rosa Island plants, *D. nana* Moran ex P. Thomson. Moran (personal communication 1994) thinks it would be better to refer to the name as *D. nana* P. Thomson (incorrectly attributed to Moran). Thomson based his description of *D. nana* on Moran's (1951) unpublished description of "forma *nana*" and on material of the cultivar 'White Sprite' (Thomson, personal communication, March 1994). Thomson (1993) mentioned 'White Sprite' without referring to collection data. In the late 1970s, Abbey Garden named

and distributed *D. greenei* 'White Sprite,' which they had propagated from a cutting or plant given to them by Dorothy Dunn (Higgs, personal communication 1996). She obtained her material from Reid Moran. The International Succulent Institute distributed Moran 3364 (from UC Berkeley) as 'White Sprite' in 1977 (Kimnach and Lyons 1977).

Thomson published the name *D. nana* Moran ex P. Thomson without citation of a type specimen. In the description there was no discussion regarding the reasons for recognizing this taxon separate from *D. greenei*. The arrow on the map on p. 197 is an accurate approximation, but the table on p. 17 (Thomson 1993) incorrectly lists *D. nana* as occurring on Santa Cruz Island, rather than on Santa Rosa Island. The lack of collection number, collector, collection date, type specimen, or location of a type specimen in an herbarium indicate Thompson's protologue did not constitute a valid publication according to the International Code of Botanical Nomenclature in effect at the time (Greuter 1988) or according to the Code in effect now (Greuter 1994).

In his monograph, Thomson described 12 new species and made 11 new combinations. He recognized most taxa previously named as subspecies (and many taxa previously reduced in synonymy) as full species. He separated *Hasseanthus* from *Dudleya* as had been done prior to 1953 (Thomson 1993; Uhl and Moran 1953; Moran 1951, 1953). In Thomson's book, there are references to only seven herbarium specimens and to one set of duplicates for those seven. Although I disagree with Thomson on several other points, for reasons mentioned below, I do think the plants he referred to as *D. nana* are distinct enough to be recognized at the species level.

SPECIES TREATMENT

Dudleya gnoma S. McCabe, sp. nov. (Fig. 1).—Type: USA, California, Santa Barbara Co., Santa Rosa Island, approximately 200 m W of East Point, found in shallow soils on top of a bare, rocky knoll, elevation 20 m, 7 May 1993, ex hort 20 May 1993, S.W. McCabe 792 (holotype: CAS; isotypes: SBBG, UC).

Plantae caespitosae ad 10 cm latae. Rosulae 8–51 mm latae. Caulices 5–26 mm longae diametro (1.5–)12–20 mm. Rosulae foliis 8–19, triangularis vel trianguli-ovatis, 6–25 mm longis, 5–13 mm latis, acutis, glaucis. Rami floriferi, 25–129 mm alti 2–5 mm crassi. Folia caulina 10–15, triangularia, turgida, 5–10 mm longa, 4–6 mm lata, acuta, glauca. Rami 2 vel 1–3 simplices vel bifurcati. Pedicelli 1–3 mm longi. Calyces segmentis triangularis 3.5–4 mm longis 2–3 mm latis, acutis, glaucis. Petala ca. 1–2 mm connata, elliptica, 8–9(–11) mm longa, 3 mm lata, flavus-aureus, acuta. Filamenta

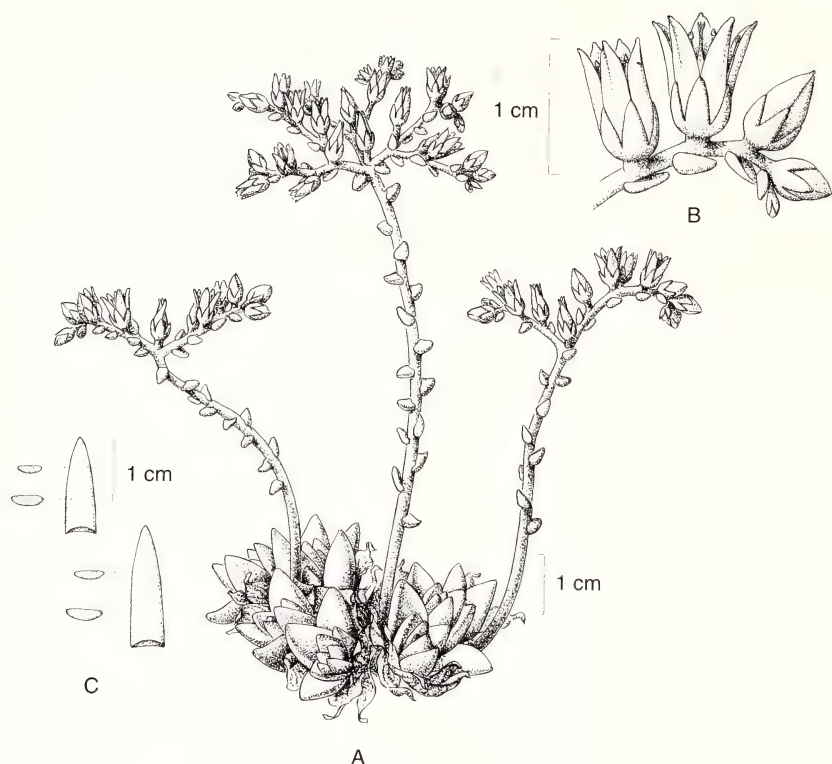


FIG. 1. *Dudleya gnoma*. A, entire plant. B, detail of flowers. C, leaves and cross-sections. All from McCabe 792, drawn primarily in Jun 1993 from live plants used as isotypes and using photos of the holotype. Drawing by Carol Barner, 1993.

6.5–8 mm longa. Carpella erecta. Ovarii 4–6 mm longis. Stylis 2–3 mm longis. Chromosomatum numerus $n=34$.

Low, cryptically colored succulent plants to 10 cm across. Roots shallow, rapidly tapering. Rosettes 1–57; 8–51 mm in diameter. Caudex caespitously branching, 5–26 mm long \times (1.5–)12–20 mm thick; maximum of 12 mm between branches; covered below rosette with dried leaves; caudex and leaf bases not changing to burgundy-purple in response to leaf removal or other wounding. Leaves 8–19 per rosette; tinged with burgundy color underneath wax, especially on leaf tips; triangular or triangular-ovate; (6–)9–25 mm long \times 5–13 mm wide; convex abaxially, plane or concave or slightly convex adaxially; leaf margins acute adaxially; apices acute; faces heavily glaucous, single wax line on adaxial surface apparently from “bud-printing”. Floral stems usually with 2 branches, occasionally

1 or 3 or more, rebranching 0–1 time; terminal flower of inflorescence 0–2 mm from point of branching; cincinni spreading initially to horizontal or recurved as flowers mature; 25–129 mm long \times 2–5 mm thick; glaucous; lightly tinged with burgundy; 0–24 mm to first leaf. Floral stem leaves 10–15 per inflorescence; changing to burgundy-purple in response to leaf removal or other wounding; horizontal to 20° above perpendicular to axis; triangular, 5–10 mm long \times 4–6 mm wide; turgid, clasping, acute. Pedicels erect, 1–3 mm long. Sepals lightly tinged with burgundy; tips red-burgundy or greenish-yellow; triangular, 3.5–4 mm long \times 2–3 mm wide; acute; glaucous. Petals fused 1–2 mm; slightly twisted in bud; erect to slightly outcurving at tips, some flowers with petals ascending-erect with upper margins not quite touching, scarcely outcurved at tip; pale yellow to bright yellow, often tinged slightly with red especially on and near keel and towards petal tips—on some appearing almost orange; elliptic, 8–9(–11) mm long \times 3 mm wide, acute; lightly glaucous on keels, especially towards tips. Stamens 6.5–8 mm long, epipetalous shorter by less than 0.5 mm. Nectar glands 1 mm. Ovaries 4–6 mm long; styles 2–3 mm long. Seeds fusiform, flattened on one side, tapering more on one end; 0.7–1.0 mm long. Chromosome number $n=34$ (C. H. Uhl in Uhl and Moran, 1953). The epithet, derived from New Latin, means diminutive, fabled being and refers to the small size of the plants and their parts.

PARATYPES: USA, California, Santa Barbara Co., Santa Rosa Island, “Thin gravelly soil of a barren knoll 200 yards from East Point, Santa Rosa Island (near 33°56.5'N, 119°58.2'W”. voucher for Dr. Uhl’s chromosome count, 13 Mar 1950, ex hort 8 Jun 1951 *Reid Moran 3364* (UC 015364); ex hort 15 Jun 1950, some of the flower stalks appear etiolated, *Moran 3364* (UC 918949); ex hort. 8 Jun 1951, *Moran 3364* (SBBG) formerly housed at SBM; on bare, ridge several hundred meters west of East Point, 40 m west of East Point bench mark, 7 May 1993, ex hort Apr 1994, *McCabe 794* (CAS); 400–500 m W of East point, the middle of the three known colonies, petals in bud with some red, 7 May 1993, *McCabe 795* (US).

Additional information on the plant description. The differences between Moran’s (1951) description and my field notes are probably a reflection of individual variation between plants and the differences between field-grown and cultivated specimens. In cultivation, plants of *McCabe 792* had leaves up to 4 mm longer and rosettes 13 mm wider than recorded in the field. Moran’s (1951) description differed in minor details from my field notes and those details have been incorporated above and in Table 1. Some plants of this species in cultivation more than 10 years (e.g., *McCabe 179*) have caudices that have become longer and have thus branched more often than those I saw in the wild. Because collection data were not certain,

measurements from *McCabe 179* were not included in the description. In low light, inflorescences elongate, petals may become less erect, and the leaves become somewhat more lanceolate and less triangular than in field-collected plants.

Habitat. *Dudleya gnoma* occurs on low, rounded hills at elevations of 20–70 m on the extreme southeast portion of Santa Rosa Island on gravelly, poorly developed, very shallow volcanic soils, where it is essentially the only higher-plant species. The otherwise bare patches of ground where this *Dudleya* grows are surrounded by low grassland vegetation.

Substrate. Several rocks collected from the surface of the soil at the type location and from outcrops at the highest colony are Miocene volcanoclastic sandstones. This contrasts with the Monterey formation, a diatomaceous rich formation, which has been mapped as the predominant rock type in the vicinity of *D. gnoma* on the southeastern tip of the island (Dr. Robert Garrison, UCSC Earth Sciences, personal communication, 1994). McEachern (1994) noted several other rock types in the bare patches. Further field work is needed.

Distribution and population size. *Dudleya gnoma* is known only from the type locality and two additional colonies within a few hundred meters west of the type locality. The type locality occupies an area less than 34 m × 12 m. Sarah Chaney and I estimated the total number of known plants on 7 May 1993 to be roughly 3200. Totals for the farthest east and west colonies were estimated and the total for the middle colony was counted (230 individuals).

Inclusion in subgenus Dudleya. *Dudleya gnoma* differs from other members of subg. *Dudleya* by having some flowers on some plants more wide-spreading than flowers of typical members of the subgenus, approaching the petal attitude of members of subg. *Stylophyllum*, such as *D. traskiae*. The open, relatively flat habitats and very shallow soils *D. gnoma* inhabits are typical of habitats occupied by members of subg. *Hasseanthus*. In other respects, such as the evergreen nature of the plants, broad leaf bases, and petal attitude of the “average” flower, *D. gnoma* is most similar to members of subg. *Dudleya*. Although the division of species into subgenera in this genus may be artificial due to possible reticulate evolution, *D. gnoma* is placed in subg. *Dudleya*.

Comparison with other taxa. *Dudleya gnoma* differs from *D. greenei* by its smaller rosettes and shorter, mostly triangular to triangular-ovate leaves vs. larger, variously shaped leaves that are not triangular (See Table 1). *Dudleya gnoma* has shorter stem leaves, smaller flowers, and shorter pedicels than in *D. greenei*. In the in-

florescences of *D. gnoma*, the base of the pedicel of the first flower is usually 2–4 mm from the base of the lowest cincinnus. In *D. greenei* the base of the pedicel of the first flower may be 0–5 mm from the base of the first cincinnus, but it is usually 0 mm, i.e., at the base of the first cincinnus.

In *D. gnoma*, there are usually two branches to the inflorescence and the two infrequently rebranch. In *D. greenei*, there are usually three inflorescence branches, which more often rebranch and become more upright (ascending) as the cincinni uncurl. In the field in 1993, some *D. gnoma* had inflorescences with additional branching below the main floral branches. Such branching occurs normally in some species, such as *D. edulis* and occasionally (after heavy rain years or under lush horticultural conditions) in other species, such as *D. greenei*, *D. caespitosa*, and *D. lanceolata*. In the last three species the additional branches arise below what would normally be the first flower and depart from the floral stem at an angle slightly above the horizontal rather than ascending as in typical primary inflorescence branches. The production of some secondary branches in *D. gnoma* and *D. greenei* (observed in 1993) may have resulted from the wet winter of 1992–1993. Even the smallest flowering plants of *D. greenei* (McCabe 798), which looked quite young, differed from *D. gnoma* by having blunter leaf apices and leaves more oblong and more rounded in cross-section.

The habitat of relatively level, bare, shallow soil contrasts with the habitats of *D. greenei*, which are usually steep, rocky coastal cliffs, steep areas with rocky soils, or canyons. Unlike the easily visible bright white or green leaves of *D. greenei* on the common habitats of reddish-brown soil or dark colored cliffs, *D. gnoma* is cryptically colored and inconspicuous in its habitat. Although *D. gnoma* is very similar in color to the glaucous forms of *D. greenei*, *D. gnoma* is difficult to spot even though it grows with few other species of higher plants and on fairly level ground. Non-glaucous forms have not been found in *D. gnoma*, but both glaucous and non-glaucous forms are common in *D. greenei*.

At the population of *D. greenei* found closest to East Point (near the Torrey Pine Grove), only a few plants of *D. greenei* were even beginning to flower when plants of *D. gnoma* appeared to be past the halfway point of their blooming season. There thus appears to be at least some temporal and geographic isolation of *D. gnoma* from *D. greenei*. The steep cliffs below the upper East Point colony were not examined for additional *Dudleya* plants.

Dudleya greenei is a polymorphic species not always easily distinguished from *D. candelabrum*. *Dudleya candelabrum* differs from *D. gnoma* in much the same manner noted previously for *D. greenei*, although plants of *D. candelabrum* tend to be even larger (Table 1). Additionally, *D. candelabrum* differs from *D. gnoma* by the pres-

TABLE 1. COMPARISON OF MEMBERS OF *DUDLEYA* SUBG. *DUDLEYA* FOUND ON SANTA ROSA ISLAND. Some measurements of *D. greenii* and *D. candelabrum* include data for these species from adjacent islands as well. Measurements from Moran (1951) are included in the table.

| | <i>D. gnoma</i> | <i>D. greenii</i> | <i>D. candelabrum</i> |
|--|---|---|------------------------|
| Leaf | | | |
| length (mm) | 5-13 | 28-110 | 55-170 |
| width (mm) | 6-25 | 9-35 | 17-70 |
| thickness (mm) | 2-4 | 4-8 | 4-7 |
| Rosette width (mm) | 8-51 | 50-150 | 100-300 |
| Floral stem leaf | | | |
| length (mm) | 5-10 | 10-30 | 30-70 |
| width (mm) | 4-6 | 5-12 | 10-20 |
| shape | triangular; thick | lanceolate to oblong, \pm thick | lanceolate, \pm thin |
| attitude | 0-20° above horizontal | 0-20° above horizontal | 90-0° below horizontal |
| Inflorescence | | | |
| thickness (mm) | 2-5 | 3-13 (usually 5.5-9) | 6-10 |
| length (mm) | 25-129 (1 at 291 in cult.) | 110-500 | 150-540 |
| no. of branches | usually 2, occasionally 3 | usually 3, rarely 2 | usually 3 or more |
| Base of 1st pedicel from 1° infl branch (mm) | rarely 0, usually 2-4 | usually 0 (0-5) | 0 |
| Caudex thickness (mm) | 1.5-17 | 14-50 | 20-100 |
| Petal attitude | erect (to ascending-erect in cultivation) | erect, (to ascending-erect in cult.) tips slightly out-curved | erect, tips outcurved |
| Flowering | May-June | June-July | June-July |

ence of thick caudices that are swollen at the base, usually quite long, reflexed floral stem leaves, usually green leaves, and three or more branches to the inflorescences. The habitat for *D. candelabrum* is steep, inland to coastal canyons, often north-facing or shaded cliffs, and often on deeper soils than *D. greenei*.

Dudleya gnoma is clearly separate from *Dudleya caespitosa*. *Dudleya caespitosa* is very similar to *D. greenei*, differing chiefly by its bright yellow flowers as opposed to usually pale yellow flowers and by more variation in leaf shape and size. Phenotypic dwarf forms of *D. caespitosa* have been found in San Mateo County, approximately 430 km north-northwest of *D. gnoma*. The morphology of the dwarf forms grade into normal forms in the area. The dwarf plants of *D. caespitosa* respond more vigorously to cultivation than do those of *D. gnoma*; they further differ by having the base of the pedicels of the first flowers at the base of the cincinni, brighter yellow and more erect petals, broader leaf apices, and less glaucous leaves.

The various forms of *D. greenei* and *D. caespitosa* respond well to summer water. When *D. gnoma* receives supplemental summer water it retains its leaves as usual, but there is little new growth and the roots may actually be killed. In summary, compared with what may be its closest relatives, *D. greenei* and *D. caespitosa*, *D. gnoma* is unusual in its habitat requirements, petal attitude, short and thin-stalked inflorescences, and near-obligate summer dormancy period.

Even though *D. gnoma* grows only 2 km from *D. blochmaniae* subsp. *insularis* in somewhat similar habitats, it differs from its close neighbor by not possessing an underground corm, by having broad rather than narrow leaf bases, by having evergreen rather than vernal leaves, and by having fairly upright rather than widespreading petals.

Dudleya parva grows on the mainland adjacent to the location of the Channel Islands. Like *D. gnoma*, *D. parva* is a dwarf member of subg. *Dudleya* and also appears to be restricted to Miocene volcanic substrates. *Dudleya parva*, however, has narrower, less glaucous summer-deciduous leaves and is restricted to north-facing slopes.

Specimens from Prince Island (off San Miguel Island), topotypes of *D. hoffmannii* Johansen and *D. regalis* Johansen, are clearly different from *D. gnoma*, but within the range of variation for *D. greenei*. The leaves of *D. hoffmannii* were described (Johansen 1932a, b) as over twice the length of those of *D. gnoma*. The leaves of *D. regalis* were described as over four times as long.

Although *D. echeverioides* Johansen has been described as having an odor "unmistakably resembling that of woodland violets" (Johansen 1935), I noticed no such odor from any member of subg. *Dudleya* on the island. Johansen's (1935) description of *D. eche-*

verioides with leaves linear, spatulate, or oval, 34–45 mm long and obtuse and having inflorescences with several branches, differs from the triangular to lanceolate, acute leaves 6–25 mm long and 2–3 branches of the inflorescences found in *D. gnoma*. Therefore, *Dudleya echeverioides* clearly differs from *D. gnoma*.

Glaucous plants in D. candelabrum. Although it has been previously reported that *D. candelabrum*, another northern Channel Island endemic, is non-glaucous (Moran 1951, Munz 1968, and Bartel in Hickman 1993), I found somewhat glaucous plants of *D. candelabrum* on Santa Cruz Island (McCabe 692 and McCabe 694) and heavily glaucous plants on Santa Rosa Island that appeared in other respects to be *D. candelabrum* (McCabe 801). The leaves were 55–97 mm long, the caudices 45 mm thick, and the floral stem leaves were reflexed on some of the inflorescences. These and other plants of *D. candelabrum* are easily distinguished from plants of *D. gnoma*. Seed germination and seedling establishment were poor for seeds of McCabe 801 (out of 30 seeds, 1 seedling survived to one month and then died) indicating the possibility of low fertility in this plant.

Taxonomic rank. With the segregation of *D. verityi* (Nakai 1983) and the recognition of *D. palmeri* separate from *D. caespitosa* (e.g., Bartel 1993 and Munz 1968), the main characteristic separating *D. caespitosa* from *D. greenei* is petals bright yellow vs. petals pale yellow. (I also consider the red-petaled plants of southern Monterey County to be more similar to *D. palmeri* than to *D. caespitosa* in most cases.) The discovery of relatively bright yellow petals in *D. greenei* (e.g., McCabe 803 on Santa Rosa Island below the Torrey Pine Grove) further lessens the distinction between *D. caespitosa* and *D. greenei*. Even though plants from near the Torrey Pine Grove could possibly be considered to be *D. caespitosa*, they are left as *D. greenei* as had been done by Uhl and Moran (1953).

Because of the minor differences between *D. caespitosa* and *D. greenei*, the possibility that *D. greenei* could later be reduced to a subspecies of *D. caespitosa*, and because of the differences between *D. gnoma* and other species, it makes more sense to treat *D. gnoma* as a species than as a subspecies. Although an argument could be made to treat it as a subspecies of *D. greenei*, *D. gnoma* is more easily separable from all other species and subspecies than the following species pairs are from each other: *D. farinosa*/*D. caespitosa*, *D. caespitosa*/*D. palmeri*, *D. caespitosa*/*D. greenei*, and *D. greenei*/*D. candelabrum*.

Threats. *Dudleya gnoma* is threatened by erosion, at least during heavy rain years. Large, non-native grazing mammals such as cattle, elk, and deer probably exacerbate this erosion. In 1993, approximately 5% of the plants were uprooted in some sections. Later sam-

pling by Park Service research staff (McEachern 1994) yielded results similar to my estimates. For example, McEachern (1994) found the colonies to have the following percentages of uprooted plants: lower 5.0%, middle 3.6%, and upper 9.0%. I noted many broken floral stems (perhaps from hooves or small animal herbivory). Although I found some small plants with single rosettes indicating some reproduction, I saw no first-year seedlings. Given the small population size, the uprooted plants, and the apparent slow rate of replacement, there is cause for concern about the long-term viability of the populations.

The National Park Service has placed a fence around the colonies since work on this article began. Uprooted plants have also been replanted.

Additional specimens examined. My specimens will be housed at CAS and collection numbers, unless otherwise noted, are mine.

Dudleya greenei Rose.—USA, California, Santa Barbara Co., San Miguel Island: Prince Island off of San Miguel Island, 10 May 1932, *Ralph Hoffmann* (holotype of *D. hoffmannii*, CAS); Prince Island, 10 May 1932, *Hoffmann* (syntype of *D. regalis*, CAS); Prince Island, $n=51$, 30 Jun 1950, *Moran* 3443, 3443A (topotype of *D. regalis*, UC, CAS); San Miguel Id., North Point, 29 Jun 1950, *Moran* 3440 (UC); Hoffmann Cliff (Eagle Cliff), $n=51$, 27 Jun 1950, *Moran* 3438 (UC, CAS). Santa Cruz Island: Jul and Aug 1886, *Edw. L. Greene* (holotype, CAS); Pelican Bay, 1 May 1931, *Ira W. Clokey* 5358 (UC, CAS); Pelican Bay, $n=34$, “1935?, cultivated at La Canada, California,” *Moran* 242 (UC); north coast, e. of West Point, near the top of a near-vertical cliff, 21 May 1991, 754. Santa Rosa Island: “Vicinity of Bletcher’s Bay,” 30 Jun 1931, *L. R. Abrams* and *I. L. Wiggins* 222 and 243 (UC, CAS, SBBG); Arlington Cyn. 550', $n=51$, ex hort 19 Jun 1950, *C. F. Smith* 2537A (UC); Water Canyon, on canyon slope, 1 1/2 miles inland, 5 Dec 1930, *Ralph Hoffmann* (Note this is the same year, collector, and island as lost *D. echeverioides* type, but there is no indication that this was a type. CAS); above Cherry Canyon, on a ridge top, on shallow soil above a *Lyonothamnus floribundus* var. *asplenifolius* grove, 8 May 1993, 798; at the base of the *Pinus torreyana* grove, at the base of a dry streambed/dry cascade, 12 m above the main road, 9 May 1993, 803.

D. candelabrum Rose.—USA, California, Santa Barbara Co., Santa Cruz Island, Jul and Aug 1886, *Edw. L. Greene* (holotype, CAS); Santa Cruz Island, Willows Anchorage, $n=17$, 11 Mar 1950, ex hort 2 Jun 1951, *Moran* 3354; near Valley Anchorage, first small arroyo e. of stairs, 9 Apr 1990, 692; in canyon near 50–100 m north of Rancho del Sur, 9 Apr 1990, 694. Santa Rosa Island, mouth of Old Ranch Canyon, $n=17$ count by Uhl, 8 Apr 1941, *Moran* 829; mouth of Old Ranch Canyon, mouth of marsh, n.-facing cliffs, elev. 3 m, 31 May

1996, 858; mouth of Cherry Canyon, n.-facing slope, overlooking NPS compound, growing near *D. greenii*, 9 May 1993, 802; along road 0.65 km by road n. of "road's end" at Johnson's Lee, 8 May 1993, 799; 4 km e. by road of Johnson's Lee, near mouth of Jolla Vieja Canyon, 801 very glaucous, 8 May 1993, 800, 801.

D. blochmaniae subsp. *insularis* (Moran) Moran—USA, California, Santa Barbara Co., Santa Rosa Island: Old Ranch Point, ca. 10' elev. (near 33°57.7'N, 119°58.6'W), 10 Mar, 1950, ex hort 15 Jun 1950, *n*=17 count by Uhl, *Moran* 3352 (holotype, UC); just s. of a small point, Old Ranch Point, also called "Oat Point" on some maps, elev. 3–5 m, 6 May 1993, 791.

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GENETIC DIVERSITY IN RARE AND WIDESPREAD SPECIES OF *LOMATIUM* (APIACEAE)

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ABSTRACT

Levels of genetic diversity were assessed in populations of three rare species of *Lomatium* and three of their more widespread congeners. *Lomatium rollinsii*, *L. serpentinum*, and *L. laevigatum* maintain significantly less intrapopulational isozymic variation than do the more widespread *L. dissectum*, *L. grayi*, and *L. triternatum*. The limited genetic diversity of these rare species may result from genetic bottlenecks associated with their origins and/or genetic drift in small populations. The patterns reported here support the general trend reported for many other comparisons of rare and widespread congeneric plant species.

Assessment of the genetic diversity of rare plant species has become an important component of management programs for sensitive, threatened, and endangered species. However, despite several recent studies of genetic variation in rare and widespread congeners (reviewed in Karron 1987, 1991), no clear generalizations have emerged on the levels and patterns of genetic diversity in rare plant species (Karron 1991; Hamrick et al. 1991). For example, allozymic polymorphism is absent in several rare species (e.g., *Oenothera hookeri*, Levy and Levin 1975; *Chrysosplenium iowense*, Schwartz 1985; *Pedicularis furbishiae*, Waller et al., 1987; *Howellia aquatilis*, Lesica et al. 1988; *Bensoniella oregona*, Soltis et al. 1992; *Harperocallis flava*, Godt et al. 1997), but many other rare species maintain levels of polymorphism similar to or higher than those of their more widespread congeners (e.g., *Astragalus linifolius* and *A. osterhouti*, Karron et al. 1988; *Layia discoidea*, Gottlieb et al. 1985; *Aletes humulis*, Linhart and Premoli 1993; *Delphinium viridescens*, Richter et al. 1994, unpubl. data; several species of *Polygonella*, Lewis and Crawford 1995; *Achillea millefolium* ssp. *megacephala*, Purdy and Bayer 1996). Therefore, although most narrowly endemic plant species have low to moderate levels of genetic (i.e., allozymic) polymorphism (e.g., Pleasants and Wendel 1989; Les et al. 1991; Bayer 1992; Sherman-Broyles et al. 1992; Baskauf et al. 1994; Cosner and Crawford 1994; Edwards and Wyatt 1994; Purdy et al. 1994; Purdy and Bayer 1995a, b; Godt et al. 1996; Wolf and Sinclair 1997; reviewed in Hamrick and Godt 1989 and Karron 1991), not all rare species are genetically depauperate. Furthermore, general trends in the levels and distribution of genetic variation may provide rough

guidelines for the development of conservation and management strategies, but these guidelines may not be appropriate for all species (see review by Hamrick et al. 1991). Additional genetic studies of other rare species are therefore needed both to develop specific management programs and to improve our generalizations on the genetic structure of rare plant species.

Lomatium (Apiaceae) comprises 70–80 species of herbaceous perennials from western North America (Constance 1993). Of these, nearly half would generally be considered narrow endemics. Furthermore, many of these narrow endemics would be considered “geographically restricted” rare species (sensu Rabinowitz 1981; Rabinowitz et al. 1986; Karron 1991), occupying very limited ranges and comprising perhaps fewer than five known populations and 20,000 individuals. Because of the numerous rare species in *Lomatium*, and because species of *Lomatium* appear on the lists of sensitive, threatened, and endangered plant species of several western U.S. states, we assessed the levels and patterns of genetic diversity in three species with restricted distributions (*L. rollinsii* Math. & Const., *L. serpentinum* (M. E. Jones) Math., and *L. laevigatum* (Nutt.) Coult. & Rose) and compared these data with those for samples of three of their more widespread congeners (*L. triternatum* (Pursh) Coult. & Rose, *L. grayi* Coult. & Rose, and *L. dissectum* (Nutt.) Math. & Const.).

Lomatium rollinsii is restricted to fairly mesic areas in the meadow-steppe communities (Daubenmire 1970) of southeastern Washington and adjacent Idaho. It occurs only in Asotin County, WA, and Nez Perce County, ID. *Lomatium serpentinum* occurs on granite outcrops along the Snake River and its tributaries in Asotin County, WA, Nez Perce County, ID, and Wallowa County, OR. Given its apparent habitat specificity, *L. serpentinum* would also be classified as a “sparse” species (Rabinowitz, 1981). *Lomatium laevigatum* is narrowly distributed along the Columbia River in Klickitat County, WA, and Wasco County, OR. All populations occur within the Columbia River Canyon and fall within a 15-km strip along the river.

In contrast, *L. grayi*, *L. dissectum*, and *L. triternatum* have much broader distributions. *Lomatium dissectum* is perhaps the most widespread of all species of *Lomatium*, ranging from southern British Columbia and Alberta to southern California and Arizona and from near the Pacific Coast to Colorado. Three varieties have been recognized (Hitchcock and Cronquist 1973), but these intergrade considerably and are not consistently followed. *Lomatium grayi* ranges from northcentral Washington and northern Idaho south to northeastern Nevada and occasionally to southeastern Idaho, Wyoming, and Colorado. It is particularly common on rocky outcrops and in disturbed sites throughout southern and eastern Washington and in northcentral Oregon. *Lomatium triternatum* ranges from southern

Alberta and British Columbia to northern California, Utah, and Colorado and is particularly abundant in central and eastern Washington. *Lomatium triternatum* occurs in several habitats, including those supporting the meadow-steppe, sagebrush steppe, and ponderosa pine communities of the Inland Pacific Northwest (sensu Daubenmire and Daubenmire 1968; Daubenmire 1970). Morphological differences among populations in plant architecture, leaflet width, and fruit shape in particular have been recognized taxonomically at sub-specific and varietal levels (Hitchcock and Cronquist 1973).

In this study, we examined levels of allozymic polymorphism in two or more populations of each of the rare and widespread species of *Lomatium* described above to see whether these rare species maintain lower, equivalent, or higher levels of genetic diversity than do their more widespread congeners. This information will be useful for any future management programs for the restricted species and will help to refine generalizations about the levels and patterns of genetic diversity in rare plant species.

MATERIALS AND METHODS

Plant samples. Two populations each were sampled from *L. rolinsii*, *L. serpentinum*, and *L. dissectum*, along with three populations of *L. grayi*, four of *L. laevigatum*, and seven of *L. triternatum*. Collection data and sample sizes are given in Table 1. Leaves were collected from plants in the field, stored in plastic bags, transported to the lab on ice, and stored at -80°C until electrophoresis was conducted.

Electrophoresis. Electrophoretic protocols generally followed Soltis et al. (1983). Leaf samples were removed from the ultracold and were immediately prepared for electrophoresis by grinding in the Tris-HCl grinding buffer (Soltis et al. 1983) with 12% PVP. Fourteen enzymes were assayed, although not all enzymes were strongly expressed or clearly resolved in all species: aldolase (ALD), aspartate aminotransferase (AAT), fluorescent esterase (FE), fructose 1,6-diphosphatase (F1,6DP), glyceraldehyde 3-phosphate dehydrogenase (G3PDH), isocitrate dehydrogenase (IDH), leucine aminopeptidase (LAP), malate dehydrogenase (MDH), phosphoglucoisomerase (PGI), phosphoglucomutase (PGM), 6-phosphogluconate dehydrogenase (6PGD), shikimate dehydrogenase (SkDH), superoxide dismutase (SOD), and triosephosphate isomerase (TPI). ALD, AAT, FE, LAP, PGI, SOD, and TPI were resolved on a modification (Haufler, 1985) of gel and electrode buffer system 8 (Soltis et al. 1983); IDH, MDH, PGM, 6PGD, and SkDH were resolved on buffer system 9 at pH 5.7; F1,6DP and G3PDH were resolved on buffer system 1. Staining for all enzymes followed Soltis et al. (1983), except that LAP was stained following Rieseberg and Soltis (1987).

TABLE 1. COLLECTION DATA FOR POPULATIONS OF RARE AND WIDESPREAD SPECIES OF *LOMATIUM* INCLUDED IN THIS STUDY. Sample sizes are in parentheses.

| | | | |
|-----------------------|-------------|----------------|--|
| Rare species | | | |
| <i>L. rollinsii</i> | Washington: | Garfield Co.: | <i>Soltis & Soltis</i> 2222 (32). |
| <i>L. serpentinum</i> | Washington: | Asotin Co.: | <i>Soltis & Soltis</i> 2394 (12). |
| <i>L. laevigatum</i> | Washington: | Asotin Co.: | <i>Soltis & Soltis</i> 2219 (8). |
| | | Asotin Co.: | <i>Soltis & Soltis</i> 2221 (46). |
| | | Klickitat Co.: | <i>Soltis & Soltis</i> 2189 (4). |
| | | Klickitat Co.: | <i>Soltis & Soltis</i> 2191 (18). |
| | Oregon: | Klickitat Co.: | <i>Soltis & Soltis</i> 2192 (34). |
| | | Wasco Co.: | <i>Soltis & Soltis</i> 2209 (24). |
| Widespread species | | | |
| <i>L. dissectum</i> | Washington: | Whitman Co.: | <i>Soltis & Soltis</i> 2257 (28). |
| <i>L. grayi</i> | Washington: | Whitman Co.: | <i>Soltis & Soltis</i> 2311 (24). |
| | | Whitman Co.: | <i>Soltis & Soltis</i> 2312 (24). |
| | | Whitman Co.: | <i>Soltis & Soltis</i> 2414 (31). |
| | Idaho: | Whitman Co.: | <i>Soltis & Soltis s.n.</i> (Paradise) (27). |
| <i>L. triternatum</i> | Oregon: | Idaho Co.: | <i>Soltis & Soltis</i> 2480 (32). |
| | Washington: | Wheeler Co.: | <i>Campbell et al.</i> 54 (32). |
| | | Asotin Co.: | <i>Soltis & Soltis</i> 2485 (32). |
| | | Kittitas Co.: | <i>Campbell et al.</i> 62 (32). |
| | | Lincoln Co.: | <i>Soltis & Soltis</i> 2492 (32). |
| | | Spokane Co.: | <i>Soltis & Soltis</i> 2500 (32). |
| | | Whitman Co.: | <i>Soltis & Soltis</i> 2489 (32). |

Genetic inference and data analysis. Regions of staining activity were numbered sequentially from the anodal portion of the gel, and allozymes were designated alphabetically from the most anodal allozyme in each staining region. Loci and alleles were inferred from the observed banding patterns and from the known subunit structure and subcellular compartmentalization of the enzymes (Gottlieb, 1982; Weeden and Wendel, 1989). For each population, we computed the proportion of loci that were polymorphic (P), the mean number of alleles per locus (A), and the mean (expected) heterozygosity (H).

RESULTS

Twenty-five electrophoretic loci were interpreted, although not all loci could be scored for all populations: *Ald-1*, *Aat-1*, *Fe-1*, *Fe-2*, *F1,6dp-1*, *F1,6dp-2*, *G3pdh-1*, *G3pdh-2*, *Idh-1*, *Lap-1*, *Mdh-1*, *Mdh-2*, *Mdh-3*, *Pgi-2*, *Pgm-1*, *Pgm-2*, *Pgm-3*, *6pgd-1*, *6pgd-2*, *Skdh-1*, *Sod-1*, *Tpi-1*, *Tpi-2*, *Tpi-3*, and *Tpi-4*. *Pgi-1* could not be scored reliably in any population.

Rare species. Populations of *L. rollinsii*, *L. serpentinum*, and *L. laevigatum* maintain very low levels of allozymic polymorphism (Tables 2, 3). When the duplicated TPI loci with segregating variation (*Tpi-1/2* in *L. rollinsii* and *L. serpentinum* and *Tpi-3/4* in *L. laevigatum*) are excluded, the number of polymorphic loci is reduced even further. In *L. rollinsii*, only two of 13 loci were polymorphic in population 2222 ($P = 0.154$; Tables 2, 3), and only three of 14 loci were polymorphic in population 2394 ($P = 0.214$). In *L. serpentinum*, only *Pgi-2* (of 18 loci) was polymorphic in population 2221 ($P = 0.056$), and none of the 16 loci scored for population 2219 was polymorphic ($P = 0$). Three of the four populations of *L. laevigatum* (2189, 2191, and 2209) exhibited no allozymic polymorphism at any of the 19 loci examined whereas population 2192 had two polymorphic loci ($P = 0.105$). There were no fixed differences between populations in any of the three rare species, although slight interpopulation differences in allele frequencies were detected (Table 2).

Allelic diversity, as measured by A , and mean heterozygosity are also low in the three rare species (Table 3). Populations of *L. rollinsii* maintain slightly greater diversity than do those of either *L. serpentinum* or *L. laevigatum*. Values of A ranged from 1.14 to 1.31 (mean of 1.22) in *L. rollinsii*, from 1.0 to 1.06 (mean of 1.03) in *L. serpentinum*, and from 1.0 to 1.10 (mean of 1.02) in *L. laevigatum*. Expected heterozygosities ranged from 0.021 to 0.038 (mean of 0.030) in *L. rollinsii*, from 0 to 0.005 (mean of 0.002) in *L. serpentinum*, and from 0 to 0.030 (mean of 0.008) in *L. laevigatum*.

TABLE 2. ALLELE FREQUENCIES AT ELECTROPHORETIC LOCI IN POPULATIONS OF RARE AND WIDESPREAD SPECIES OF *LOMATIUM*. Note that not all populations could be scored for all loci; dashes indicate missing data. Allelic designations represent within-species variation; no attempt was made to compare alleles between species (see text). Allelic designations for *L. triternatum* are taken from a larger study of genetic structure in that species (Soltis et al., unpublished data); therefore, not all alleles are present in the seven populations included in this study. Asterisks indicate duplicated loci with tentative allelic designations (see text); these loci were not included in calculation of genetic diversity measures.

| Rare species population | | | | | | | | | | Widespread species population | | | | | | | | | | |
|-------------------------|------|------|------|------|----------------------|------|------|------|------|-------------------------------|------|------|-----------|------|-----------------|------|------|------|------|------|
| <i>L. serpentinum</i> | | | | | <i>L. laevigatum</i> | | | | | <i>L. dissectum</i> | | | | | <i>L. grayi</i> | | | | | |
| <i>L. rollinsii</i> | 2222 | 2394 | 2219 | 2221 | 2189 | 2191 | 2192 | 2209 | 2257 | 2311 | 2312 | 2414 | Para-dise | 2480 | 2485 | 2489 | 2492 | 2500 | 54 | 62 |
| <i>Ald-1a</i> | 1.00 | 1.00 | — | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | — | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| <i>Aat-1a</i> | — | 0.12 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | — | — | — | — | — | — | — |
| <i>Aat-1b</i> | — | 0.88 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | — | — | — | — | — | — |
| <i>Fe-1a</i> | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.0 | 0.35 | — | — | — | — | — | — | — |
| <i>Fe-1b</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.00 | 1.00 | 0.65 | — | — | — | — | — | — | — |
| <i>Fe-2a</i> | 1.00 | 1.00 | — | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | — | 1.00 | 1.00 | 1.00 | 1.00 | — | — | — | — | — | — | — |
| <i>Fl6dp-1a</i> | 1.00 | — | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | — | — | 1.00 | 1.00 | — | 0.0 | 0.0 | 0.0 | 0.07 | 0.0 | 0.0 | 0.0 |
| <i>Fl6dp-1b</i> | 0.0 | — | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | — | 0.0 | 0.0 | — | 0.0 | 0.0 | 0.0 | 0.29 | 0.0 | 0.0 | 0.0 |
| <i>Fl6dp-1c</i> | 0.0 | — | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | — | 0.0 | 0.0 | — | 1.00 | 1.00 | 1.00 | 0.64 | 1.00 | 1.00 | 1.00 |
| <i>Fl6dp-2a</i> | 1.00 | — | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | — | — | 1.00 | 1.00 | — | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| <i>G3pdh-1a</i> | — | — | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | — | — | 1.00 | 1.00 | 1.00 | 1.00 | — |
| <i>G3pdh-2a</i> | — | — | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | — | — | — | — | 1.00 | 1.00 | — |
| <i>Idh-1a</i> | — | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | — | — | 1.00 | 1.00 | 1.00 | — | — | — | — | — | — | — |
| <i>Lap-1a</i> | 0.07 | 0.14 | 1.00 | 1.00 | 1.00 | 1.00 | 0.91 | 1.00 | 0.02 | 0.0 | 0.95 | 0.57 | 1.00 | 0.0 | 0.0 | 0.0 | * | 0.0 | 0.0 | 0.0 |
| <i>Lap-1b</i> | 0.88 | 0.86 | 0.0 | 0.0 | 0.0 | 0.0 | 0.09 | 0.0 | 0.15 | 0.32 | 0.05 | 0.09 | 0.0 | 0.02 | 0.0 | 0.02 | 0.02 | 0.02 | 0.03 | 0.0 |
| <i>Lap-1c</i> | 0.02 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.80 | 0.65 | 0.0 | 0.34 | 0.0 | 0.89 | 0.95 | 0.85 | 0.98 | 0.92 | 1.00 | 1.00 |
| <i>Lap-1d</i> | 0.03 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.02 | 0.02 | 0.0 | 0.0 | 0.0 | 0.09 | 0.03 | 0.02 | 0.0 | 0.05 | 0.0 | 0.0 |
| <i>Lap-1e</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.02 | 0.11 | 0.0 | 0.0 | 0.0 | 0.0 |
| <i>Mdh-1a</i> | — | — | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 0.07 | 0.14 | 1.00 | — | 1.00 | — | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 |
| <i>Mdh-1b</i> | — | — | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.39 | 0.76 | 0.0 | — | 0.0 | — | — | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |

TABLE 2. CONTINUED

| Rare species population | | | | | | | | | | Widespread species population | | | | | | | | | | | |
|-------------------------|------|------|-----------------------|------|------|----------------------|------|------|---------------------|-------------------------------|-----------------|------|-----------|----------------------|------|------|------|------|------|------|--|
| <i>L. rollinsii</i> | | | <i>L. serpentinum</i> | | | <i>L. laevigatum</i> | | | <i>L. dissectum</i> | | <i>L. grayi</i> | | | <i>L. triernatum</i> | | | | | | | |
| Locus/Allele | 2222 | 2394 | 2219 | 2221 | 2189 | 2191 | 2192 | 2209 | 2257 | 2311 | 2312 | 2414 | Para-dise | 2480 | 2485 | 2489 | 2492 | 2500 | 54 | 62 | |
| <i>Mdh-1c</i> | — | — | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.54 | 0.10 | 0.0 | — | 0.0 | — | — | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| <i>Mdh-2a</i> | — | — | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | — | — | 1.00 | 1.00 | 1.00 | — | — | 0.97 | — | — | 1.00 | 1.00 | |
| <i>Mdh-2b</i> | — | — | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | — | 0.0 | 0.0 | 0.0 | — | — | 0.03 | — | — | 0.0 | 0.0 | |
| <i>Mdh-3a</i> | 1.00 | 1.00 | — | — | 1.00 | 1.00 | 1.00 | 1.00 | — | — | — | — | — | 0.0 | 0.0 | 0.18 | 0.02 | 0.0 | 0.0 | 0.0 | |
| <i>Mdh-3b</i> | 0.0 | 0.0 | — | — | 0.0 | 0.0 | 0.0 | 0.0 | — | — | — | — | — | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| <i>Mdh-3c</i> | 0.0 | 0.0 | — | — | 0.0 | 0.0 | 0.0 | 0.0 | — | — | — | — | — | 1.00 | 1.00 | 0.82 | 0.95 | 0.87 | 1.00 | 0.77 | |
| <i>Mdh-3d</i> | 0.0 | 0.0 | — | — | 0.0 | 0.0 | 0.0 | 0.0 | — | — | — | — | — | 0.0 | 0.0 | 0.03 | 0.0 | 0.0 | 0.0 | 0.0 | |
| <i>Mdh-3e</i> | 0.0 | 0.0 | — | — | 0.0 | 0.0 | 0.0 | 0.0 | — | — | — | — | — | 0.0 | 0.0 | 0.0 | 0.0 | 0.13 | 0.0 | 0.23 | |
| <i>Pgi-2a</i> | 0.97 | 1.00 | 1.00 | 0.05 | 0.0 | 0.0 | 0.28 | 0.0 | — | — | 0.0 | 0.03 | — | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| <i>Pgi-2b</i> | 0.03 | 0.0 | 0.0 | 0.95 | 1.00 | 1.00 | 0.72 | 1.00 | — | — | 0.0 | 0.24 | — | 0.03 | 0.50 | 0.0 | 0.0 | 0.0 | 0.04 | 0.0 | |
| <i>Pgi-2c</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | — | 0.96 | 0.40 | — | 0.0 | 0.06 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| <i>Pgi-2d</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | — | 0.04 | 0.32 | — | 0.97 | 0.43 | 0.90 | 0.90 | 1.00 | 0.82 | 1.00 | |
| <i>Pgi-2e</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | — | 0.0 | 0.0 | — | 0.0 | 0.03 | 0.03 | 0.10 | 0.0 | 0.0 | 0.0 | |
| <i>Pgi-2f</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | — | 0.0 | 0.0 | — | 0.0 | 0.03 | 0.0 | 0.0 | 0.0 | 0.14 | 0.0 | |
| <i>Pgm-1a</i> | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | — | 0.73 | — | — | 0.80 | — | — | — | — | — | — | — | |
| <i>Pgm-1b</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | 0.27 | — | — | 0.20 | — | — | — | — | — | — | — | |
| <i>Pgm-2a</i> | 0.0 | 0.04 | 1.00 | 1.00 | ab* | ab* | ab* | ab* | — | 0.17 | * | * | * | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| <i>Pgm-2b</i> | 1.00 | 0.96 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | 0.83 | — | — | — | 0.0 | 0.0 | 0.14 | 0.0 | 0.0 | 0.0 | 0.10 | |
| <i>Pgm-2c</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | 0.0 | — | — | — | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | |
| <i>Pgm-2d</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | 0.0 | — | — | — | 0.77 | 0.90 | 0.84 | 0.50 | 0.68 | 0.71 | 0.79 | |
| <i>Pgm-2e</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | 0.0 | — | — | — | 0.23 | 0.10 | 0.02 | 0.47 | 0.32 | 0.29 | 0.11 | |
| <i>Pgm-2f</i> | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | 0.0 | — | — | — | 0.0 | 0.0 | 0.0 | 0.03 | 0.0 | 0.0 | 0.0 | |
| <i>6Pgd-1a</i> | 1.00 | — | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | 1.00 | — | 1.00 | 1.00 | 1.00 | — | 0.75 | — | 0.76 | — | 0.89 | — | — | |
| <i>6Pgd-1b</i> | 0.0 | — | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | — | 0.0 | 0.0 | 0.0 | — | 0.25 | — | 0.24 | — | 0.11 | — | — | |

TABLE 2. CONTINUED

| Rare species population | | | | | | | | | | Widespread species population | | | | | | | | | | | | | | | | | | | |
|-------------------------|--|--|--|--|-----------------------|--|--|--|--|-------------------------------|--|--|--|--|---------------------|--|--|--|--|-----------------|--|--|--|--|-----------------------|--|--|--|--|
| <i>L. rollinsii</i> | | | | | <i>L. serpentinum</i> | | | | | <i>L. laevigatum</i> | | | | | <i>L. dissectum</i> | | | | | <i>L. grayi</i> | | | | | <i>L. triternatum</i> | | | | |
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TABLE 3. GENETIC VARIABILITY MEASURES FOR POPULATIONS OF RARE AND WIDE-SPREAD SPECIES OF *LOMATIUM*.

| Species/ Population | <i>P</i> | <i>A</i> | <i>H</i> |
|------------------------|----------|----------|----------|
| Rare species | | | |
| <i>L. rollinsii</i> | | | |
| 2222 | 0.154 | 1.31 | 0.021 |
| 2394 | 0.214 | 1.14 | 0.038 |
| Mean | 0.184 | 1.22 | 0.030 |
| <i>L. serpentinum</i> | | | |
| 2219 | 0.0 | 1.0 | 0.0 |
| 2221 | 0.056 | 1.06 | 0.005 |
| Mean | 0.028 | 1.03 | 0.002 |
| <i>L. laevigatum</i> | | | |
| 2189 | 0.0 | 1.0 | 0.0 |
| 2191 | 0.0 | 1.0 | 0.0 |
| 2192 | 0.105 | 1.10 | 0.030 |
| 2209 | 0.0 | 1.0 | 0.0 |
| Mean | 0.026 | 1.02 | 0.008 |
| Widespread species | | | |
| <i>L. dissectum</i> | | | |
| 2257 | 0.222 | 1.56 | 0.096 |
| 2311 | 0.357 | 1.57 | 0.144 |
| Mean | 0.290 | 1.56 | 0.120 |
| <i>L. grayi</i> | | | |
| 2312 | 0.188 | 1.19 | 0.022 |
| 2414 | 0.133 | 1.33 | 0.081 |
| Paradise | 0.167 | 1.17 | 0.064 |
| Mean | 0.163 | 1.23 | 0.056 |
| <i>L. triternatum</i> | | | |
| 2480 | 0.556 | 1.67 | 0.146 |
| 2485 | 0.375 | 1.75 | 0.102 |
| 2489 | 0.462 | 1.77 | 0.109 |
| 2492 | 0.556 | 1.89 | 0.151 |
| 2500 | 0.333 | 1.33 | 0.075 |
| 54 | 0.273 | 1.45 | 0.079 |
| 62 | 0.222 | 1.33 | 0.079 |
| Mean | 0.397 | 1.60 | 0.106 |

Widespread species. Higher levels of polymorphism are maintained in populations of the more widespread species. In *L. dissectum*, population 2257 was scored for only nine loci, and two of these (*Lap* and *Mdh-1*) were polymorphic ($P = 0.222$). Population 2311 was polymorphic at five of 14 loci ($P = 0.357$): *Lap*, *Mdh-1*, *Pgm-1*, *Pgm-2*, and *6pgd-2*. In *L. grayi*, 15 loci were scored in population 2414, and 16 were scored in population 2312. *Lap* and *Pgi-2* were polymorphic in each, and *Skdh* was polymorphic in 2312 (and un-

scorable in 2414); P was 0.133 in population 2412 and 0.188 in population 2312. The Paradise population was polymorphic at two of 12 loci scored ($P = 0.167$): *Fe-1* and *Pgm-1*. In *L. triternatum*, P ranged from 0.273 to 0.462 (mean $P = 0.356$) in those three populations where 10 or more loci were scored and from 0.222 to 0.556 (mean $P = 0.427$) in the four populations where fewer than 10 loci were scored (Table 3). Furthermore, in a study of genetic diversity and population structure in 33 populations of *L. triternatum* (Soltis et al., unpublished data), levels of polymorphism ranged from 0.20 to 0.54 in those populations where at least 10 loci were scored and from 0.11 to 0.62 for those populations in which nine or fewer loci were scored. Mean values of P in the larger study were 0.389 for the 15 populations with 10 or more scorable loci and 0.420 for the 18 populations with nine or fewer scorable loci, with an overall mean of 0.406.

These more widespread species also maintain higher values of A and H than do the rare species (Table 3). Values of A ranged from 1.56 to 1.57 in *L. dissectum*, from 1.17 to 1.33 in *L. grayi*, and from 1.33 to 1.89 in *L. triternatum*. Mean values of A for *L. dissectum*, *L. grayi*, and *L. triternatum* were 1.56, 1.23, and 1.60, respectively. Values of H ranged from 0.096 to 0.144 in *L. dissectum*, from 0.022 to 0.081 in *L. grayi*, and from 0.075 to 0.151 in *L. triternatum*. Mean expected heterozygosities for populations of *L. dissectum*, *L. grayi*, and *L. triternatum* were 0.120, 0.056, and 0.106, respectively.

DISCUSSION

Comparison of genetic diversity in rare and widespread congeners. The three rare species of *Lomatium* examined in this study have significantly lower levels of intrapopulational genetic diversity than do three of their more widespread congeners. Mean levels of polymorphism (P), allelic diversity (A), and expected heterozygosity (H) are all lower in the rare species than in the widespread ones even though only two populations of *L. dissectum* and three populations of *L. grayi* were examined. This pattern of reduced genetic diversity in the rare species is maintained when other genetic markers are used. Populations of *L. laevigatum* have identical chloroplast genomes (cpDNA) and DNA sequences from the internal transcribed spacers (ITS) of nuclear ribosomal DNA, whereas *L. grayi*, *L. dissectum*, and *L. triternatum* harbor both cpDNA and ITS variation (Soltis and Kuzoff, 1993; Soltis et al. unpublished data). This pattern also conforms to that observed in many other rare and widespread congeners (reviewed by Karron 1987, 1991), although populations of some rare plant species, such as *Layia discoidea* ($P = 0.905$; Gottlieb et al. 1985) and a population of *Polygonella robusta* ($P = 0.727$; Lewis and Crawford 1995), maintain very high levels

of genetic variation. Isozymic variation was not detected in several other rare plant species (e.g., *Oenothera hookeri*, Levy and Levin 1975; *Chrysosplenium iowense*, Schwartz 1985; *Howellia aquatilis*, Lesica et al. 1988; *Pedicularis furbishiae*, Waller et al. 1987; *Bensoniella oregona*, Soltis et al. 1992; *Lacondonia schismatica*, Coello et al. 1993), but most rare species examined to date maintain low to moderate levels of genetic diversity as measured by isozymes (e.g., species of *Coreopsis*, Cosner and Crawford 1994; Purdy et al. 1994; Purdy and Bayer 1995b; Hamrick and Godt 1989; Karron 1991).

Causes of reduced genetic diversity in rare species. As reviewed elsewhere (e.g., Karron 1991; Fiedler and Ahouse 1992), many factors may act singly or in concert to reduce levels of genetic diversity in rare species. For example, historical factors such as the age of the species and past changes in its distribution may affect the levels of genetic variation present both within and among populations of the species. A species of recent origin may have a restricted distribution and may maintain low levels of polymorphism because of a recent genetic bottleneck associated with speciation. Alternatively, a relictual species may have existed sufficiently long to accumulate mutations (see Lewis and Crawford 1995), but genetic bottlenecks may have reduced current levels of diversity. Furthermore, rare species of any age are particularly susceptible to stochastic changes in allele frequency (e.g., Wright 1931, 1938, 1956; Nei et al. 1975; reviewed in Barrett and Kohn 1991, and Ellstrand and Elam 1993) and to strong selection that may reduce levels of genetic diversity across populations of a species (e.g., Babbie and Selander 1974) or eliminate rare alleles that are exposed in homozygotes that arise through increased inbreeding in small populations (e.g., Wright 1956). Furthermore, differences in life histories may contribute to differences in genetic diversity between rare and widespread congeners.

Which, if any, of these factors may be responsible, collectively or alone, for the reduced levels of intrapopulational allozymic diversity detected in rare species of *Lomatium* relative to their more widespread congeners? No apparent life-history characteristics differ between these rare and widespread *Lomatium* species, suggesting that differences in genetic diversity may more likely result from historical events and/or differences in population size. None of the three rare species appears to be of recent origin. A phylogenetic analysis of cpDNA restriction site variation in 30 species of *Lomatium*, representing all but one of the morphological groups in the genus (sensu L. Constance, personal communication), indicates that all three species are of more or less intermediate age (Soltis and Novak, 1996). Thus, genetic bottlenecks resulting from the *recent*

derivation of these rare species from more widespread and allelically diverse progenitors (sensu Gottlieb 1973, 1974) cannot be responsible for the limited genetic diversity detected in the narrow endemics. However, genetic bottlenecks could have accompanied their origins, but in the more distant past, and genetic drift in small populations is likely responsible for the maintenance of low levels of variation in these species.

CONCLUSIONS

Levels of intrapopulational genetic variation, as measured by isozymes, are significantly lower in rare species of *Lomatium* than in their more widespread congeners. This finding is similar to those reported for most other comparisons of intrapopulational genetic diversity in rare and widespread congeners. These additional data for species of *Lomatium* therefore support and strengthen the generalization that narrowly endemic plant species maintain only low levels of genetic variation. Furthermore, although only two (*L. rollinsii* and *L. serpentinum*) or four (*L. laevigatum*) populations of each rare species were sampled, only minor differences in allele frequencies were detected among populations. However, these populations may differ in attributes other than their isozyme profile (see Hamrick et al. 1991) and may be well adapted to their local environments. Possible genetic divergence in morphological, reproductive, and physiological traits, for example, should also be considered in the preparation of conservation and management strategies for all three species.

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EVALUATION OF SALT TOLERANCE AND RESIN PRODUCTION IN COASTAL AND CENTRAL VALLEY ACCESSIONS OF *GRINDELIA* SPECIES (ASTERACEAE)

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ABSTRACT

The objective of this study was to evaluate the effect of NaCl on growth of *Grindelia* accessions from coastal and inland habitats. Gas exchange, biomass and resin production, and cation accumulation were studied for two accessions of *Grindelia stricta* from coastal estuaries, one accession of *G. camporum* from the northern part of the Central Valley, and one accession of *G. camporum* from the South Coast Ranges. A greenhouse experiment was conducted in which these accessions were grown for 140 days in sand culture at 5, 125, 250, and 550 mM (\approx sea water) NaCl. No major differences in salt tolerance were found between coastal and inland accessions—both species used in this study were found to be miohalophytes. Survival at 550 mM was 10% or lower for three of the four accessions. Gas exchange (net CO₂ uptake and transpiration) was reduced at salinities above 125 mM, and biomass production was significantly affected by salinity. However, we observed moderate growth rates at salinities up to 250 mM. We also noted a trend toward increased surface resin with increased salinity, but more experiments are needed to thoroughly evaluate this response. *Grindelia* is a potential crop plant which is tolerant to high salinity but our results indicate that biomass production would be significantly reduced if *Grindelia* were cultivated in saline soils.

RESUMEN

Se evaluó el efecto del NaCl sobre el crecimiento de cuatro entradas de *Grindelia* de ambientes costeros y mediterráneos. Se estudió el intercambio de gases, la producción de biomasa y resina, y la acumulación de cationes para dos entradas de *Grindelia stricta* provenientes de estuarios costeros, una entrada de *G. camporum* de la parte norte del Central Valley, y una entrada de *G. camporum* del South Coast Ranges. Se realizó un ensayo de invernáculo en el que se cultivaron estas entradas por 140 días en un medio de arena con 5, 125, 250, y 550 mM NaCl. No se encontraron diferencias significativas en cuanto a tolerancia a la salinidad entre entradas de la costa y tierra adentro—ambas especies usadas en este estudio podrían ser consideradas miohalófitas. Se observó supervivencia de 10% o menos en tres de las cuatro entradas a 550 mM NaCl. El intercambio de gases (absorción neta de CO₂ y transpiración) se redujo a niveles de salinidad superiores a 125 mM y la salinidad afectó significativamente la producción de biomasa. Sin embargo observamos un crecimiento moderado a salinidades de hasta 250 mM. También observamos una tendencia a aumento de la resina superficial al aumentar la salinidad, aunque se necesitan más experimentos para evaluar en profundidad esta respuesta. *Grindelia* es un cultivo potencial que es tolerante de altos niveles de salinidad, pero nuestros

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resultados indican que la producción de biomasa de *Grindelia* podría reducirse significativamente si se la cultiva en suelos salinos.

The genus *Grindelia* comprises approximately 60 species of annuals, perennials, and shrubs native to North and South America. Most North American species occur in arid and semiarid areas of the Southwest, Rocky Mountains states, and along the Pacific Coast. Six species of *Grindelia* (and several varieties) are currently recognized for California by Lane (1993); previously Munz (1968), based largely on the work of Steyermark (1934), recognized 11 species. Several taxa inhabit coastal marshes in California where they grow with other halophytic species such as *Salicornia virginica* L., *Spartina foliosa* Trin., *Jaumea carnosa* (Less.) A. Gray, and *Distichlis spicata* (L.) E. Greene, among others. Populations of *Grindelia camporum* E. Greene can be found in saline habitats in the Central Valley of California, associated with species of such salt-tolerant genera as *Atriplex*, *Suaeda*, *Distichlis*, and *Heliotropium*.

Grindelia species have been studied as potential crop plants because they produce a diterpenoid resin on the stems, leaves and involucres that may have value in the naval stores industry, with applications including inks, adhesives, tackifiers, and synthetic polymers (Hoffmann and McLaughlin 1986; Hoffmann et al. 1984). The production of surface resins by plants probably is an adaptation to aridity since most species that produce such resins are xerophytes (Hoffmann et al. 1984). Surface resins can protect leaves from excessive transpiration (Meinzer et al. 1990) and prevent the development of extreme leaf temperatures by increasing reflectance. More information is needed to better understand the ecological significance of surface resins and the effect of the environment, including salinity, on resin production.

Grindelia camporum, in particular, has been investigated as a potential crop for arid lands because it combines a high resin content (Timmermann et al. 1987) with good biomass yield and relatively low irrigation requirement (McLaughlin and Linker 1987). Tolerance of high soil salinity would also be a valuable trait in a new crop because it would permit its cultivation in areas where soils have degraded due to salinization. Salt tolerance in *G. camporum* likely could be improved by selection among accessions for salt tolerance. Alternatively, increased salt tolerance might be incorporated into *G. camporum* by hybridization with coastal salt-marsh *Grindelia* species that presumably have greater salt tolerance.

Based on their occurrence in saline habitats, some *Grindelia* species are clearly able to tolerate moderate to high salt concentrations in the soil. However, the manner in which salt affects their growth is not known. Growth could be depressed as in miohalophytes which tolerate salt but have optimum growth on fresh water, or it could be

stimulated by NaCl in concentrations as high as 200 mM (about two fifths of that of sea-water) as in euhalophytes (Glenn and O'Leary, 1984). Furthermore, the effect of NaCl concentration on the secretion of resin is not known.

To better understand salt tolerance in *Grindelia*, we studied the influence of NaCl on growth, gas exchange, cation content, and resin in four accessions. We were particularly interested in comparing the salt tolerance of coastal and inland taxa. We selected accessions that we believed should show a range of variation in their response to salt: two came from coastal estuaries, one was from the northern part of the Central Valley, and one was from the South Coast Ranges. We hypothesized that the salt-marsh accessions would prove to be euhalophytes, that the Central Valley accession would be a miohalophyte, and that the South Coast Range accession would have the lowest salt tolerance.

MATERIALS AND METHODS

Plant materials. Four accessions were included in this experiment: *G. camporum* var. *camporum* (SPM 6547; 2N = 24), collected in the Sacramento River Valley along State Route 20 east of I-5 in Colusa County; *G. camporum* var. *camporum* (SPM 6560; 2N = 24), collected in the South Coast Range east of Highway 101 on State Route 58 near Santa Margarita in San Luis Obispo County; *G. stricta* DC. var. *stricta* (SPM 6548; 2N = 24), collected from an estuary of Humboldt Bay adjacent to Elk River Road east of Highway 101 in Humboldt County; and *G. stricta* var. *platyphylla* (E. Greene) M. A. Lane (SPM 6558; 2N = 24), collected from an estuary just north of Moss Landing along State Route 1 in Monterey County. The collections of *Grindelia camporum* var. *camporum* from near Colusa and Santa Margarita will be referred to as *G. camporum* COL and *G. camporum* SM, respectively. Bulk seed collections, obtained by gathering seed from several plants in each population, were made between 22 and 25 September 1991. Voucher specimens were deposited at ARIZ.

Experimental conditions. Seeds were germinated in the greenhouse in 1-in. pots containing sand and peat moss (1:1 by volume) after a pre-treatment of one week in water at 3°C with exposure to light. Greenhouse temperatures ranged between 32°C during the day and 12°C during the night. Three weeks after germination, 40 plants of each accession (for a total of 160 plants) were transplanted to 1-gal pots filled with pure sand. Irrigation with ½ Hoagland solution (Hoagland and Arnon 1938) was initiated three days after transplanting.

Plants were randomly assigned to one of four salt treatments: 5 mM NaCl, 125 mM NaCl, 250 mM NaCl, and 550 mM NaCl; the

latter is equivalent to the salt levels in sea water. NaCl (analytical reagent) was added at increments of 50 mM/day, starting on 31 August. Final salt concentrations were reached on 31 August, 2 September, 4 September, and 10 September for the 5, 125, 250, and 550 mM treatments, respectively. All plants were irrigated with a solution that included $\frac{1}{2}$ Hoagland solution and the NaCl at the assigned level. Solution pH was measured each time fresh solution was prepared and ranged from 6.4 to 6.5 for all solutions. Pots were irrigated three times/day with 150 ml of solution each time to allow for leaching and to prevent salt accumulation in the pots.

Gas exchange measurements. Net CO₂ uptake and transpiration were measured on 8 November on five plants of each accession growing at 5, 125, and 250 mM, using an ADC-LCA3 portable infrared gas-exchange system (Analytical Development Company, Hoddesdon, England). For the 550 mM treatment gas exchange could only be measured on *G. s. var. stricta* since there were not enough plants alive of the other accessions to permit repeated measurements. All measurements were taken in the greenhouse between 11:00 AM and 12:30 PM.

Biomass production. Five plants per species per treatment were harvested on 2 November and 28 December, 84 and 140 days, respectively, after highest salinity was reached. The aboveground portion of *Grindelia* plants consists initially of basal rosettes from which one or more leafy reproductive stems eventually bolt. Here we report all aboveground biomass as "shoots." Harvested plants were air-dried to constant weight in the greenhouse for seven to ten days after which dry weights of both shoots (DWS) and roots (DWR) were recorded. At each harvest date the numbers of bolted stems, flower-buds, and flowers at or beyond anthesis were recorded.

Resin extraction. Above-ground biomass of each harvested plant was ground to 3-mm particle-size and a 3- to 5-g subsample was extracted twice with 150 ml of dichloromethane at room temperature for 24 hr. The crude extracts were evaporated and the total crude resin yields were determined as percentage of dry biomass.

Determination of cations. Samples (0.05 g) of shoot and root tissues from the first (2 November 1994) harvest were digested overnight in concentrated nitric acid and then heated for an hour at 100 C. Na⁺, K⁺, Ca²⁺, and Mg²⁺ were determined by atomic absorption spectroscopy (Association of Official Analytical Chemists, 1984).

Statistical analysis. A factorial analysis of variance (ANOVA) with accessions (4 levels) and salt concentration (3 levels for most ANOVAs since few plants survived at 550 mM NaCl; see Results) as the main factors was done for each variable measured. The num-

ber of replicates was $n=5$ for each treatment combination. Mean separation was done using Duncan's Multiple Range test.

RESULTS

Survivorship. No mortality was observed in any accession with NaCl concentrations up to 250 mM. At 550 mM all 10 *G. s. var. stricta* plants were alive (100% survival) at 84 days, but only six *G. s. var. platyphylla*, four *G. camporum* COL, and two *G. camporum* SM (60%, 40%, and 20% survival, respectively) plants survived. At this first sampling date, five of the ten *G. s. var. stricta* plants were harvested. Surviving plants of the other accessions were not harvested to permit continued observations on survival. When the experiment was terminated at 140 days, three of the five unharvested *G. s. var. stricta* plants from the 550 mM NaCl treatment were alive (60% survival), but only one plant each of *G. s. var. platyphylla* and *G. camporum* COL survived; none of the 10 plants of *G. camporum* SM survived.

Gas exchange measurements. Averaged over the four accessions, net CO₂ uptake (A) was significantly reduced by salt concentrations higher than 125 mM ($F = 8.46$, $P < 0.01$; Fig. 1a). The four *Grindelia* accessions used in this experiment did not differ significantly in their photosynthetic response to salt, although the A rates of all *G. s. var. stricta* plants at 550 mM NaCl were higher than that of the one plant of *G. camporum* COL surviving at this salinity. Transpiration (E) was significantly affected by NaCl concentration levels above 125 mM ($F = 11.26$, $P < 0.01$; Fig. 1b) and differed among accessions ($F = 5.51$, $P < 0.01$). Transpiration rates peaked at 125 mM for all accessions but *G. camporum* SM. Overall, *G. camporum* SM showed significantly higher E rates than the other three accessions. Significant reductions in stomatal conductance (Gs) were found at NaCl concentrations above 125 mM ($F = 16.93$, $P < 0.01$; Fig. 1c), but the four *Grindelia* accessions did not differ in stomatal conductance averaged across salt treatments.

Biomass production. At first harvest, 84 days after the highest salinity was reached, DWS ($F = 44.91$, $P < .01$; Fig. 2a), DWR ($F = 32.68$, $P < .01$; Fig. 2b), and DWT (total dry weight) ($F = 41.48$, $P < .01$) were significantly affected by salt treatments in all *Grindelia* accessions. Increased salinity resulted in proportionally larger percentage reductions in DWR than in DWS, although NaCl concentration did not have a significant effect on shoot:root (S:R) ratio at the first harvest. The accessions differed significantly in their S:R ratios ($F = 8.43$, $P < 0.01$, Fig. 2c), however; *G. s. var. platyphylla* had the highest S:R ratio and *G. camporum* SM had the lowest S:R ratio.

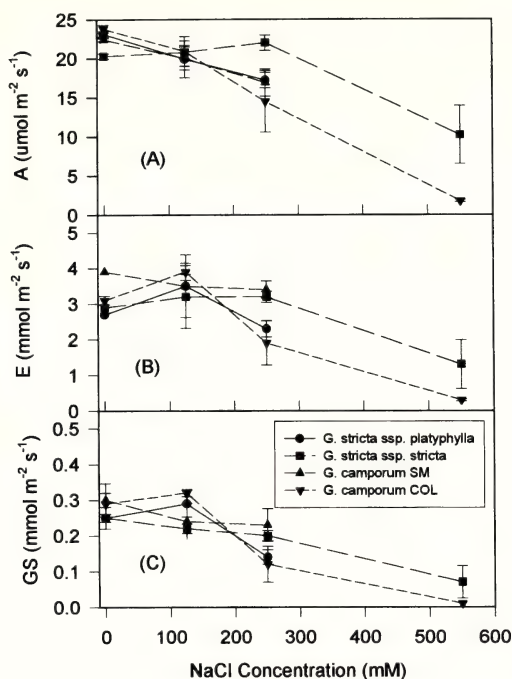


FIG. 1. Effect of NaCl on gas exchange in four *Grindelia* accessions: (A) net CO_2 uptake; (B) transpiration; (C) stomatal conductance. Error bars represent ± 1 SE of the mean; $n=5$.

At the second harvest date, 140 days after maximum salinity was reached, NaCl had a significant effect on DWS ($F = 102.84$, $P < 0.01$; Fig. 3a), DWR ($F = 115.04$, $P < 0.01$; Fig. 3b), and DWT ($F = 135.54$, $P < 0.01$). Accessions differed in their response to NaCl ($F = 9.83$, $P < 0.01$). *Grindelia s. var. platyphylla* had significantly higher DWS production than the other three accessions; *G. s. var. stricta* had the lowest DWS. Both *G. s. var. platyphylla* and *G. camporum* COL had a significantly higher DWR than *G. s. var. stricta* and *G. camporum* SM at 5 mM NaCl ($F = 8.06$, $P < 0.01$; Fig. 3b). The percentage reductions in DWS, DWR, and DWT at 125 mM NaCl and 250 mM were similar for all four accessions. One of the few clear differences found between estuarine and inland *Grindelia* accessions used in this study was that both varieties of *G. stricta* had significantly larger ($F = 11.50$, $P < 0.01$; Fig. 3c) S:R ratios at 140 days than both accessions of *G. camporum*. In the *G. stricta* varieties S:R ratios were higher at 125 mM than at 5 mM, while in the *G. camporum* accessions S:R ratios decreased with increasing salinity ($F = 11.50$, $P < 0.01$).

The number of stems bolting per plant at 84 days was significantly

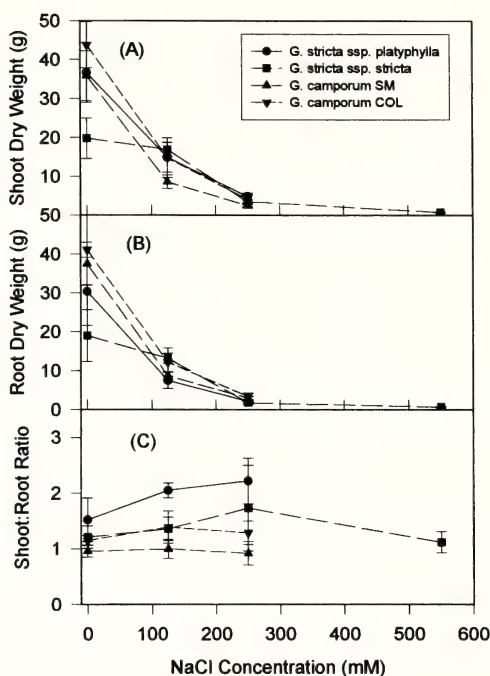


FIG. 2. Effect of NaCl on biomass accumulation of four *Grindelia* accessions measured 84 days after highest salinity was reached: (A) shoot dry weight; (B) root dry weight; (C) shoot:root ratios. Error bars represent ± 1 SE of the mean; $n=5$.

affected by NaCl concentration ($F = 34.61$, $P < 0.01$; Fig. 4a). *Grindelia s. var. platyphylla* and *G. camporum* COL had more stems per plant than the other two accessions ($F = 15.76$, $P < 0.01$). At 250 mM all *G. camporum* COL plants had bolted, all *G. camporum* SM plants were still in the rosette stage, and only one *G. s. var. platyphylla* and one *G. s. var. stricta* had produced stems (with 4 and 1 stem, respectively). The number of stems per plant at 140 days also decreased with increasing NaCl concentrations ($F = 10.82$, $P < .01$, Fig. 4b). There were also significant differences between accessions ($F = 2.92$, $P < .05$); both *G. camporum* accessions had more shoots per plant than the two *G. stricta* varieties. At 140 days only plants of the two *G. camporum* accessions had produced many flowers. Differences in numbers of flowers were noted among plants of the two accessions—*G. camporum* COL plants had an average of 15.2, 9.0, and 0 capitula per plant at 5 mM, 125 mM, and 250 mM NaCl, respectively, while those of *G. camporum* SM had 23.4, 19.6, and 1.0 capitula per plant at these salinity levels.

Resin production. A significant effect of NaCl concentration on crude resin production was found on plants harvested 84 days after

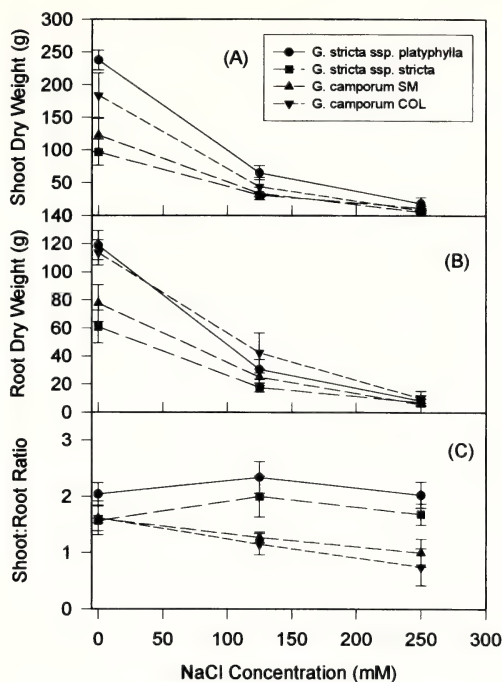


FIG. 3. Effect of NaCl on biomass accumulation of four *Grindelia* accessions measured 140 days after highest salinity was reached: (A) shoot dry weight; (B) root dry weight; (C) shoot:root ratios. Error bars represent ± 1 SE of the mean; $n=5$.

higher salinity was reached ($F = 5.45$, $P < 0.01$; Fig. 5a). The highest levels of crude extracts were found at 250 mM NaCl for *G. camporum* COL. Crude resin content was highest on plants grown at low NaCl levels in *G. camporum* SM, while there was no significant effect of NaCl on resin production in *G. s.* var. *stricta*. At 140 days there appeared to be a trend of increased crude resin content with increased salinity for all accessions but *G. stricta* var. *stricta* (Fig. 5b), although the differences were not statistically significant.

There were significant differences between accessions in crude resin contents both at 84 days ($F = 49.8$, $P < 0.01$) and at 140 days ($F = 18.1$, $P < 0.01$). Averaged across salt treatments, crude resin contents were highest for *G. camporum* COL and lowest for *G. stricta* var. *stricta*. Timmermann et al. (1987) reported the same pattern for plants sampled from the wild: high crude resin contents from plants in the Colusa population of *G. camporum*; low crude resin contents from plants in the Humboldt Bay population of *G. stricta* [reported in Timmermann et al. (1987) as *G. stricta* ssp. *blakei* (Steyserm.) Keck]; and intermediate crude resin contents in *G.*

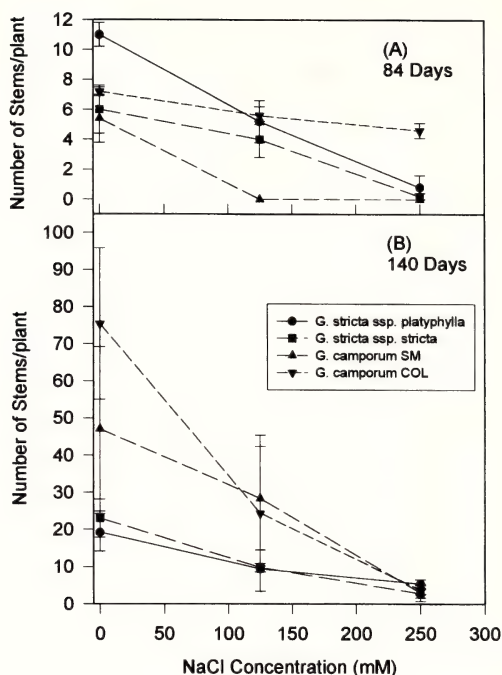


FIG. 4. Effect of NaCl on the number of stems per plant of four *Grindelia* accessions: (A) 84 days and (B) 140 day after highest salinity was reached. Error bars represent ± 1 SE of the mean; $n=5$.

camporum plants from Santa Margarita and *G. stricta* var. *platyphylla* [reported as *G. latifolia* Kell. ssp. *platyphylla* (Greene) Keck].

Cation contents. The general patterns of cation concentrations were similar for both roots and shoots: $[\text{Na}^+]$ increased, $[\text{Ca}^{2+}]$ decreased (drastically in the case of roots), and shoot $[\text{K}^+]$ decreased (Table 1). $[\text{Mg}^{2+}]$ and the ratio $[\text{K}^+]:[\text{Na}^+]$ also decreased as NaCl level increased from 5 mM to 125 mM ($P < 0.01$ for all cations; Table 1). Few significant differences were found in root cation concentrations in plants grown at 125 mM and 250 mM, except that $[\text{Ca}^{2+}]$ decreased for all four accessions and $[\text{Na}^+]$ and $[\text{K}^+]$ decreased in *G. s.* var. *platyphylla*.

The accessions differed in root $[\text{Na}^+]$, $[\text{K}^+]$, and $[\text{Mg}^{2+}]$, but not in $[\text{Ca}^{2+}]$. $[\text{Na}^+]$ and $[\text{Mg}^{2+}]$ were higher in *G. s.* var. *stricta* roots than in the other three accessions ($P < 0.01$). An interaction between NaCl concentration and accession was found for $[\text{K}^+]$ ($P < 0.01$)—as NaCl increased, $[\text{K}^+]$ fluctuated in *G. camporum* COL and *G. s.* var. *platyphylla*, and decreased in *G. s.* var. *stricta* and *G. camporum* SM.

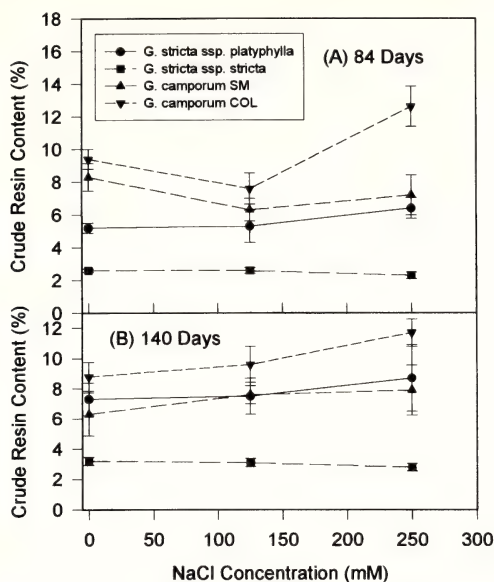


FIG. 5. Effect of NaCl on crude resin content of four *Grindelia* accessions: (A) 84 days and (B) 140 days after highest salinity was reached. Error bars represent ± 1 SE of the mean; $n=5$.

For shoots, $[\text{Na}^+]$ was higher in plants grown at 125 mM than at 5 mM NaCl but no significant differences were found between plants grown at 125 mM and 250 mM NaCl (Table 1; $P < 0.01$). $[\text{K}^+]$ and $[\text{Ca}^{2+}]$ decreased with increasing salinity ($P < 0.01$; Table 1). No significant differences were found in shoot $[\text{Mg}^{2+}]$ content or the ratio $[\text{K}^+]:[\text{Na}^+]$ between plants grown at 125 mM and 250 mM. Shoots of the four accessions differed in their $[\text{K}^+]$, $[\text{Ca}^{2+}]$ and $[\text{Mg}^{2+}]$ and in the $[\text{K}^+]:[\text{Na}^+]$ ratio. *Grindelia s. var. stricta* had higher $[\text{K}^+]$ and $[\text{Ca}^{2+}]$ than the other three accessions ($P < 0.01$), and $[\text{Mg}^{2+}]$ in *G. camporum SM* was significantly higher than in the other accessions ($P < 0.01$). Both *G. s. var. stricta* and *G. camporum SM* had higher $[\text{K}^+]:[\text{Na}^+]$ ratios than *G. s. var. platyphylla* and *G. camporum COL* ($P < 0.01$).

DISCUSSION

Accessions of *Grindelia* collected from estuary, Central Valley lowland, and foothill habitats generally responded similarly to salinity—a somewhat surprising result. All four accessions had 100% survival and positive growth rates at NaCl levels of up to 250 mM. However, survival was higher for *G. s. var. stricta* at 550 mM NaCl than for the other three accessions. Although survival rates at this NaCl concentration were very low for *G. s. var. platyphylla* and *G.*

TABLE 1. SHOOT AND ROOT CATION CONCENTRATIONS OF FOUR *GRINDELIA* ACCESSIONS GROWN UNDER THREE SALINITY LEVELS. Cation concentrations are in $\mu\text{g g}^{-1}$; salinity levels are 5, 125, and 250 mM NaCl. Means within a row (shoots and roots analyzed separately) not followed by the same letter are significantly different at $P < 0.05$.

| Accession | Cation | Shoots | | | Roots | | |
|-------------------------------|--------|---------|--------|---------|--------|--------|--------|
| | | 5 | 125 | 250 | 5 | 125 | 250 |
| <i>G. s. var. stricta</i> | Na | 101 b | 695 a | 781 a | 490 b | 805 a | 759 ab |
| | K | 1202 a | 916 b | 436 c | 674 a | 371 b | 211 b |
| | Mg | 43 a | 34 b | 29 b | 133 a | 57 b | 46 b |
| | Ca | 289 a | 252 a | 196 b | 1446 a | 880 b | 77 c |
| | Total | 1636 ab | 1897 a | 1441 b | 2744 a | 2113 b | 1093 c |
| <i>G. s. var. platyphylla</i> | Na | 106 b | 772 a | 886 a | 318 c | 752 a | 548 b |
| | K | 807 a | 569 b | 304 c | 327 ab | 495 a | 206 b |
| | Mg | 45 a | 34 ab | 31 b | 84 a | 55 b | 44 b |
| | Ca | 240 a | 189 b | 151 b | 1753 a | 1027 b | 88 c |
| | Total | 1199 b | 1564 a | 1373 ab | 2482 a | 2329 a | 887 b |
| <i>G. camporum</i> COL | Na | 105 b | 671 a | 744 a | 273 b | 582 a | 724 a |
| | K | 846 a | 584 b | 365 c | 358 a | 436 a | 381 a |
| | Mg | 47 a | 38 ab | 33 b | 103 a | 43 b | 48 b |
| | Ca | 245 a | 181 b | 141 b | 1438 a | 862 b | 75 c |
| | Total | 1252 a | 1404 a | 1331 a | 2173 a | 1923 a | 1218 b |
| <i>G. camporum</i> SM | Na | 76 b | 672 a | 764 a | 216 b | 503 a | 562 a |
| | K | 854 a | 464 b | 346 b | 403 a | 371 ab | 251 b |
| | Mg | 65 a | 53 ab | 47 b | 79 a | 48 b | 48 b |
| | Ca | 261 a | 215 ab | 173 b | 1402 a | 809 b | 71 c |
| | Total | 1252 a | 1404 a | 1331 a | 2100 a | 1731 b | 931 c |

camporum COL, some individuals of each accession were still able to endure sea-level salt concentration.

All accessions showed declines in dry matter production of both shoots and roots with increasing salinity. Differences were observed between coastal and inland accessions in the S:R ratios, however. We found an increase in the S:R ratio for both *G. stricta* accessions growing at 125 mM compared to those of plants at 5 mM. On the other hand, steady reductions in the S:R ratios as salinity increased were found for *G. camporum* accessions harvested at 140 days. The higher S:R ratios for the *G. stricta* accessions were an arithmetic consequence of a lower percentage reduction in their shoot biomass compared to their root biomass. We interpret these differences in S:R ratios as evidence that the estuary accessions were somewhat less stressed than the inland accessions by increasing soil salinity.

Net CO₂ uptake and transpiration were significantly reduced only at NaCl levels above 125 mM for *G. s.* var. *platyphylla* and both *G. camporum* accessions. Net CO₂ uptake and transpiration for *G. s.* var. *stricta* were not affected by NaCl concentrations up to 250 mM. Furthermore, even at 550 mM this accession maintained instantaneous values of CO₂ uptake above 10 $\mu\text{mol m}^{-2} \text{sec}^{-1}$ and moderate transpiration rates. Since assimilation was not affected up to 125 mM NaCl, the decrease in biomass yield with increased salinity (from 5 mM to 125 mM) could be due to energy losses through increased respiration. Reduced biomass production accompanied by increased respiration rates at higher salinities have been found in several species (Amthor 1989).

The responses of stomatal conductance to salinity corresponded to those of CO₂ uptake and transpiration, suggesting stomatal limitations to gas exchange. Such stomatal limitations have been suggested as the main cause for reduced CO₂ uptake in other halophytes (Flanagan and Jefferies 1988). However, based on analysis of CO₂ dependence curves developed by Farquahar and Sharkey (1982), Pearcy and Ustin (1984) found that both stomatal and mesophyll limitations contributed to reduced CO₂ uptake in *Spartina* and *Scirpus*, two tidal-marsh plants.

Cation accumulation is a common response to increased salinity in halophytes (Flowers et al. 1977, 1986). Salt accumulation in the cell or vacuole is part of the mechanism for osmotic adjustment in these species, although high [Na⁺] in the plant can be toxic. Moderate Na⁺ accumulation is typical of miohalophytes while euhalophytes tend to accumulate large amounts of Na⁺ and maintain their [K⁺]:[Na⁺] ratios (Glenn and O'Leary 1984). In this study, we did not find an increase in cation contents in *Grindelia* grown at moderate to high NaCl levels, although significant changes in the relative proportions of cations were found. Modest accumulation of Na⁺ and a large reduction in the [K⁺]:[Na⁺] ratios in both shoots and roots

when NaCl levels increased from 5 mM to 125 mM suggest salt exclusion at the root level. Also, the extreme reduction in $[Ca^{2+}]$ content of the roots may be an indication of possible toxic effects of NaCl for *Grindelia*. Similar changes in cation composition with increased salinity within estuarine and inland *Grindelia* accessions suggest similar physiological mechanisms for coping with salt stress in these species.

Although *Grindelia* accessions were tolerant of moderate to high salinity levels, the highest biomass production for all accessions was found on fresh water. This result further serves to characterize *Grindelia* species as miohalophytes, which tolerate high salinity but show optimum growth at very low salinities, rather than euhalophytes, which require moderately high levels of salt for optimum growth (Glenn and O'Leary 1984). We expected to find differences in the responses of coastal and inland accessions to salinity. Because the estuarine species presumably are exposed to higher levels of salinity in their native habitat we expected that they would be euhalophytes, such as the *Salicornia* spp. which are found in the same community, and that the inland accessions would have a response to salinity more typical of miohalophytes. Although euhalophytes are more common in estuary environments, other estuarine species besides *G. stricta* are miohalophytes (Glenn and O'Leary 1984), including *Isocoma menziesii* (Hook. & Arn.) G. Nesom, *Hibiscus palustris* L., *Koeleria virginica* (L.) Presl, and *Scirpus robustus* Pursh (Pearcy and Ustin 1984). Low salinity during the wet winter months of the growth season has been suggested to explain how *Scirpus robustus* survives in tidal marshes in California (Pearcy and Ustin 1984). In the case of *Grindelia stricta*, however, most growth occurs in the summer and fall months.

We found a variable response of crude resin production to increased salinity. At 84 days, the higher resin content in plants of both *G. camporum* accessions grown at 5 mM NaCl compared to that of plants grown at 125 mM and 250 mM could be the consequence of differences in phenological development; several of the plants grown at 5 mM had bolted producing stems and capitula-buds, while only one *G. camporum* (both accessions) plant had bolted at 125 mM. The difference in phenological stages may have resulted in the high resin content found in low salinity plants, since the capitula of *G. camporum* have resin contents up to 20–30% while leaves and stems are lower in resin (less than 10%) (Timmermann and Hoffmann 1985). On the other hand, the higher resin content of *G. camporum* (both accessions) grown at 250 mM compared to those at 125 mM was found in plants at similar phenological stages and thus could be a true response to salinity.

By the time of the second harvest, both accessions of *G. camporum* had bolted at all salinity levels, although the number of plants with inflorescences and the number of inflorescences per plant de-

creased with increased salinity. Any direct effect that NaCl could have on resin production (i.e., the trend of increased resin at higher salinity for *G. camporum* COL in Fig. 5b) would be masked by differences in the number of capitula produced. In this experiment our primary objective was to compare salt tolerance and biomass production, and to accomplish this objective plants were harvested at the same time. To further study the effects of NaCl on resin production, harvests should be done according to phenological stages (i.e., at peak flowering).

Grindelia s. var. *stricta* did not show any significant change in resin content with salinity. Although the dichloromethane extract has been termed "crude resin", this accession has a very low proportion of resin acids in the DCM extract (Timmermann et al. 1987). The ecological significance of the low crude resin yield and the small proportion of diterpene acids in the extract for this species is not clear to us.

There are several implications from this study for the development of *Grindelia* as a potential crop for saline soils. First, *Grindelia camporum* is able to tolerate moderate to high levels of NaCl, but biomass production is reduced at salt levels around one fourth that of sea water. Such reduced biomass production would sharply decrease the economic attractiveness of this plant as a crop for saline soils. Second, there would seem to be no advantage in hybridizing inland or foothill *G. camporum* with coastal *G. stricta* and selecting among the progeny as a means for improving the salt tolerance of *G. camporum*, since the two species appeared to be fairly similar in their responses to increased salinity. Any slight gain in salt tolerance probably would be achieved at the cost of greatly reduced resin yield. Finally, we observed a slight increase in resin production at higher salinity levels. Information on the effect of NaCl on the secretion of secondary metabolites is very scarce. Hajibagheri et al. (1983) found thicker, larger wax plates in the surface of *Suaeda maritima* leaves grown with sodium chloride. Increased production of secondary metabolites in response to stress has been reported for other plants as well (Allen et al. 1987; Benzioni et al. 1989; Vaadia et al. 1961). In this experiment we found evidence that supports this proposition, although further experiments should be conducted in order to thoroughly evaluate the response of surface resin production to NaCl.

ACKNOWLEDGMENTS

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**ATRIPLEX ERECTICAULIS (CHENOPODIACEAE): A NEW
SPECIES FROM SOUTH-CENTRAL CALIFORNIA**

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ABSTRACT

Atriplex erecticaulis is a newly described annual species from dry lowlands in south-central California. It is a hexaploid species apparently most closely related to *A. cordulata* Jepson. All collections have been from Tulare, Kern, and Kings counties in uncultivated areas. Although limited in geographic and ecological distribution it is often abundant in non-cultivated natural areas.

Atriplex erecticaulis, sp. nov., a distinctive annual species of *Atriplex* with abundantly branched, erect stems was first collected by the senior author ca. one kilometer west of Earlimart in Tulare Co. California on 26 August 1989. It was collected previously in this same area in 1921 by H. M. Hall and in 1937 by R. E. Hoover. Earlier collections were also made by Elizabeth McClintock in 1963, by Jack Zaninovich in 1963 and in 1971, and by John Thomas Howell and Gordon H. True in 1967, in a vernal-pool natural-area about 8 km east-northeast of Pixley, Tulare Co. California. Each of these earlier collections was labelled *Atriplex cordulata* Jepson, a species that resembles *A. erecticaulis* in several attributes.

***Atriplex erecticaulis* Stutz, Chu & Sanderson sp. nov. (Fig. 1)—**

TYPE: USA, California, Tulare Co., ca. 500 m west of Earlimart, T23S R25E S33, elevation ca. 100 m, 16 Oct 1994, *H. C. Stutz 9691* (holotype, BRY).

Herbae annuae. Caulis erectus, maxime ramosus, 30–50 cm altus; rami teretes nec costati nec striati, furfuracei juventute. Folia Kranz-typorum anatomiis, sessilia, alterna, cordata, deltoideo-ovata usque ovato-lanceolata, 5–15 mm longa, 5–12 mm lata, oblique patula, apice breviter acuminata, basi rotunda usque cordata, aliquando leviter amplexicaulia, integra, raro margine infra medium 1–2 irregulariter serrata, furfuracea utrinque; costa et pas lateraliis nervus

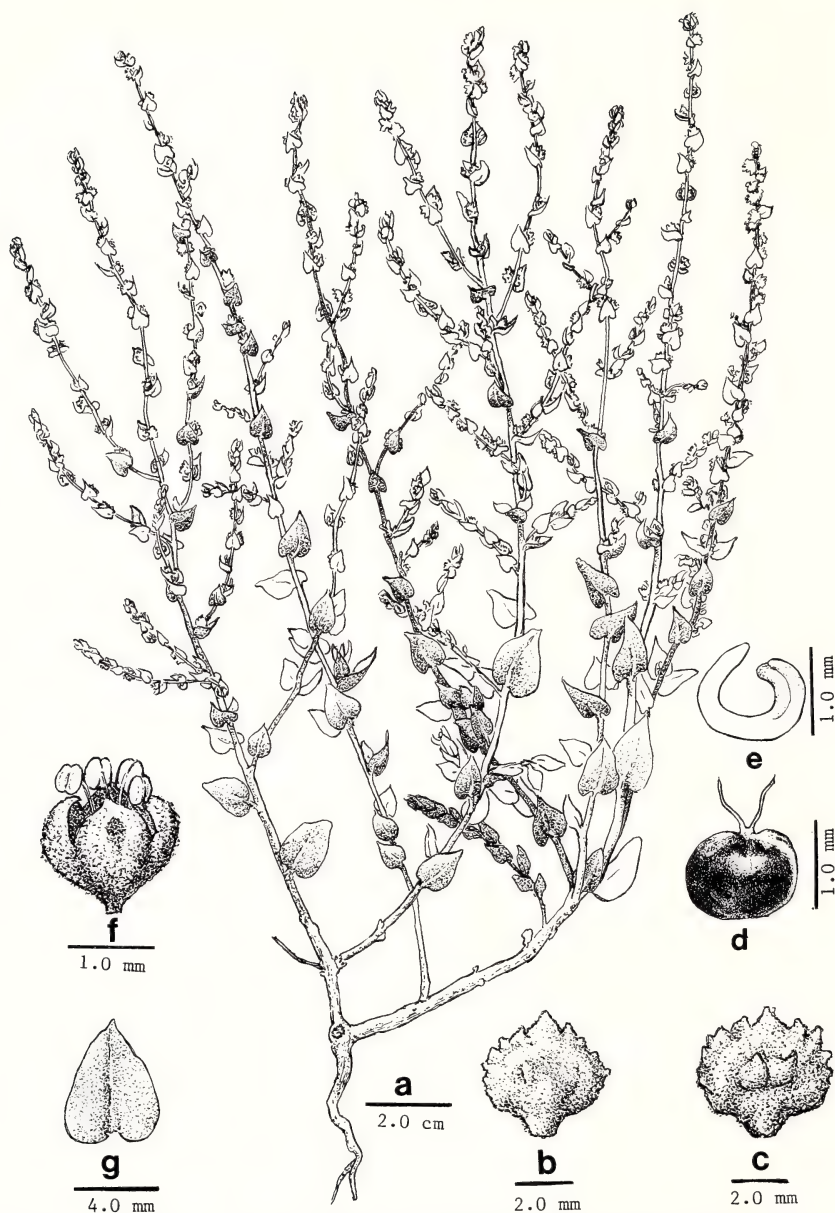


FIG. 1. *Atriplex erecticaulis*. a. Habit. b. Fruiting bract without appendages c. Fruiting bract with appendages. d. Utricle. e. Embryo. f. Male flower. g. Leaf. (Illustrations by Marcus A. Vincent.)

prominulus infra. Staminales et pistillati flores mixiti in glomerulum, axillares in ramorum partibus superioribus; perianthium staminalis floris subglobosum, ca. 1.5 mm diam. 4-partium, raro 5-partium; segmenta ovato-oblonga, ca. 1 mm longa, membranacea, furfuracea, dorsaliter apice leviter carnosa et viridia; stamina tot quot segmenta, antheris obovato-oblongis, 0.8–1 mm longis, filamentis filiformibus, ca. 1.5 mm longis, pistillo rudimentali punctiformi; bracteola pistillatis floris unita margine infra medium; stigma 2; stylus obscurus. Fructiferae bractae deltoideo-rhombeae usque flabellatae, 3–3.5 mm longae, 3–4 mm latae, dense furfuraceae, margine supra medium denticulatae, medio dente quam 2 contigui laterales dentes leviter maiori, basi et ad centrum leviter induratae, utrinque exappendices vel 1–2 irregularibus tuberculis. Utriculus transverso-oblongus or suborbicularis, ca. 1.5 mm latus, pericarpio membranaceo. Semen atrobruneum, perispermio duro; radícula supera. Chromosomatum numerus $2n=54$.

Annual herbs. Stems erect, highly branched, 30–50 cm tall, terete, not ribbed nor striate, furfuraceous when young. Leaves sessile, commonly appressed to branches, alternate, deltoid-ovate to ovate-lanceolate, 5–15 mm long, 5–12 mm wide, apex short acuminate, base rotund to cordate, sometimes slightly clasping, entire, margin sometimes with 1–2 pair of irregular teeth below the middle, midrib and one pair of lateral veins prominent on abaxial surface, furfuraceous on both surfaces, Kranz-type venation. Plants monoecious; male and female flowers in mixed glomerules, axillary on upper branches; perianth of staminate flowers subglobose, ca. 1.5 mm in diameter, 4- rarely 5-parted, segments ovate-oblong, ca. 1 mm long, covered with elongate hairs, spreading when flowering, slightly fleshy and green dorsally near apex, margin membranaceous; stamens as many as perianth segments, anthers obovate-oblong, 0.8–1 mm long, yellow, filaments filiform, ca. 1.5 mm long, slightly broadening and united toward base, pistil rudimentary, punctate; fruiting-bracts deltoid-rhombic to flabellate, compressed, united below the middle, 3–3.5 mm long, 3–4 mm wide, densely furfuraceous, slightly indurate centrally near base, mostly unappendaged, rarely with a few irregular tubercles on both surfaces, upper margin denticulate, middle tooth same size as lateral teeth or slightly larger. Utricle transverse-oblong or suborbicular, ca. 1.5 mm across, pericarp membranaceous, stigmas 2, ca. 1.2 mm long, style obscure. Seed dark-brown, perisperm farinose, radicle superior. Flowering and fruiting period: August–October. Chromosome number: $2n=54$.

PARATYPES: USA, California, Kern Co., SE corner of junction of Rowlee Rd and Pond Rd, very bushy, 5 Aug 1995, *H. C. Stutz* 9785 (BRY). Kings Co., ca. 12 mi W of Tulare, 30 Aug 1994, *H. C. Stutz* 9655 (BRY). Tulare Co., 3 mi S of Pixley, Airport St., 5 Oct 1995,

H. C. Stutz 9844 (BRY); Pixley National Wildlife Refuge, abundant roadside and inside Refuge, 5 Aug 1995, *H. C. Stutz 9788* (BRY); 1 mi W of Earlimart, 29 Jun 1995, *H. C. Stutz 9770* (BRY); Harmon field, westside of Pixley, T23S R25E S6, 16 Oct 1994, *H. C. Stutz 9692* (BRY); ½ mi W of Pixley, 30 Aug 1994, *H. C. Stutz 9656* (BRY); 1 mi W of Pixley, 30 Aug 1994, *H. C. Stutz 9652* (BRY); 1 mi W of Earlimart, 28 Aug 1994, *H. C. Stutz 9645* (BRY); ¼ mi W of Earlimart, 9 Oct 1993, *H. C. Stutz 95967* (BRY); 10 mi W of Earlimart, 18 Aug 1990, *H. C. Stutz 95354* (BRY); 1 km W of Earlimart, very, very abundant, 26 Aug 1989, *H. C. Stutz 95141* (BRY); Pixley Nature Conservancy Preserve, common in dry area, 8 Aug 1971, *Jack Zaninovich 73-338, 73-335* (CAS); vernal-pool natural-area in Valley Grassland, about 4½ mi east-northeast of Pixley, elev. 275 ft, 15 May 1968, *John Thomas Howell and Gordon True 44465* (CAS); vernal-pool natural-area in Valley Grassland, about 4½ mi east-northeast of Pixley, elev. 275 ft, 3 Nov 1967, *John Thomas Howell 44062, 44071, 44031, 44078, 44079, 44080* (CAS); vernal-pool natural-area in Valley Grassland, about 4½ mi east-northeast of Pixley, elev. 275 ft, 21 Sep 1967, *John Thomas Howell and Gordon H. True 44009, 44010, 44011, 44012, 44013* (CAS); vernal-pool natural-area in Valley Grassland, about 4½ mi east-northeast of Pixley, elev. 275 ft, 21 Sep 1967, *John Thomas Howell and Gordon True 44008* (CAS); vernal-pool natural-area in Valley Grassland, about 4½ mi east-northeast of Pixley, 10 Aug 1967, *John Thomas Howell and Gordon True 43724, 43725* (CAS); vernal-pool natural-area in Valley Grassland, about 4½ mi east-northeast of Pixley, 6 Jul 1967, *John Thomas Howell and Gordon True 43234, 43211* (CAS); Pixley Natural Area, about 5 mi east-northeast of Pixley, 40 acres of vernal pools owned by the Nature Conservancy, 22 Jun 1967, *Elizabeth McClintock* (CAS); vernal-pool natural-area in Valley Grassland, about 4½ mi east-northeast of Pixley, elev. 275 ft, 31 May 1967, *John Thomas Howell and Gordon True 42514* (CAS); Jack Zaninovich property: 40 acre vernal pool area near Pixley, ½ mi N of Ave 104 on road 124, much branched, Sep 1963, *Jack Zaninovich* (CAS); Jack Zaninovich property: 40 acre vernal pool area ½ mi N of Ave 104 on Rd 124, 3 Aug 1963, *Elizabeth McClintock* (CAS); Earlimart, 10 Aug 1937, *R. E. Hoover 2676* (UC); Earlimart, 10 Oct 1921, *H. M. Hall 11786* (UC, CAS).

Distribution and habitat. *Atriplex erecticaulis* appears to be restricted in distribution to an area of about 3000 km² in Tulare, Kern, and Kings Counties, California, at elevations below 100 meters. It is particularly abundant in the Pixley National Wildlife Refuge southwest of Pixley and in the Pixley Nature Conservancy, ca. 8 km east-northeast of Pixley. It is also abundant south of Pixley and west

TABLE 1. CONTRASTING CHARACTERISTICS OF *ATRIPLEX ERECTICAULIS* AND *A. CORDULATA*.

| Characteristic | <i>A. erecticaulis</i> | <i>A. cordulata</i> |
|--------------------------|--|-----------------------|
| Habit | bushy | strict |
| Branching | profuse | sparse |
| Flowering period | Aug and Sep | Jun and Jul |
| Anther color | yellow | purple or red |
| Fruiting-bract shape | deltoid-rhombic to flabellate | broadly deltoid-ovate |
| Fruiting bract dentation | central and lateral teeth, ca. same size | central tooth largest |
| Chromosome number | 2n=54 | 2n=36 |

of Earlimart in fields that appear to have never been cultivated. In vernal-pool areas in Tulare County, it is common on dry sites between vernal-pool depressions but not within the depressions. Roadside populations are present along the Gun Club Road ca. 15 km west of Wasco, Kern Co., California, along Airport Street ca. 5 km south of Pixley, and along Sierra Ave. ca. 5 km west of Earlimart, Tulare county.

Although *A. erecticaulis* is now apparently restricted to a relatively small geographic area, it may have had a much wider distribution prior to recent agricultural practices that have destroyed its habitat. However, its current abundance in preserves and in areas that are not subject to cultivation, suggests that its immediate survival is not being threatened.

Taxonomic Relationships. *Atriplex erecticaulis* appears to be most closely related to *A. cordulata* Jepson. They both have sessile, cordate leaves, upright, robust growth habit, and 4-(rarely 5-)parted male flowers. As shown in Table 1, they differ in several significant attributes including chromosome number, flowering periods, anther color, fruiting-bract shape (Fig. 2), fruiting-bract dentation (Fig. 2), and growth habit. The "robust and much branched bushy plants" mentioned by Hall and Clements (1923, p. 271) as a distinct form of *A. cordulata* probably refer to *A. erecticaulis* plants. This is particularly likely since Hall's collection #11786 (UC) Earlimart, Tulare County, CA, labelled *A. cordulata*, is clearly a specimen of *A. erecticaulis*.

A. erecticaulis is the only reported native annual hexaploid species of *Atriplex* in California. Other *Atriplex* species that grow in the vicinity of *A. erecticaulis* are either tetraploid (*A. cordulata*, *A. coronata* Wats., *A. trinervata* Jepson), or diploid (*A. elegans* (Moq.) Diet., *A. miniscula* Standley, *A. serenana* Nels.). (All counts were determined from pollen-mother cells taken from anthers fixed in 5%



FIG. 2. Fruiting bracts of *Atriplex cordulata* (left) and *A. erecticaulis* (right).

acetic acid, stored in 70% ethyl alcohol and squashed in acetocarmine stain.)

Flowering of *A. erecticaulis* is mostly in August and September, considerably later than all associated *Atriplex* species. Plants of *A. erecticaulis* grown in greenhouses and nurseries at Brigham Young University, Provo, Utah from seeds collected from plants growing in natural populations, had the same characteristics as plants growing in nature, including a late flowering period, suggesting high heritability of their distinctive attributes.

ACKNOWLEDGMENTS

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COASTAL SAGE SCRUB SERIES OF WESTERN RIVERSIDE COUNTY, CALIFORNIA

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ABSTRACT

The widely used term "Riversidian sage scrub" distinguishes coastal sage scrub in interior cismontane southern California from stands elsewhere but does not account for the considerable variation among stands within the region. Coastal sage scrub classification has generally emphasized either regional or floristic variation. We collected data at 181 coastal sage scrub sites in western Riverside County and classified them using multivariate cluster analyses of structural and floristic variables of shrub canopies. Roughly half of the sites fell into seven coastal sage scrub "series," largely comparable to the six interior basin "associations" described by Kirkpatrick and Hutchinson (1977). Our analysis splits Kirkpatrick and Hutchinson's *Artemisia californica*-*Eriogonum fasciculatum*-*Salvia apiana* association into three series; we did not sample their *Lepidospartum squamatum*-*Eriodictyon crassifolium*-*Yucca whipplei* association; and we recognize a deerweed series not sampled in their work. Similarities to the earlier analysis indicate that classification of this vegetation is largely repeatable, while discrepancies result from differing methodology and interpretation. The large proportion of unclassified plots suggests that these series represent segments of continua rather than discrete communities. We encourage land use planners to recognize variation among coastal sage scrub series within geographic regions to assure adequate conservation planning.

INTRODUCTION

No two stands of vegetation are identical, and classification is often ambiguous because types may grade into one another along continua. Colinvaux (1993:406–412) rejects vegetation classification and the notion of the plant community. Yet community-level management may be "the only viable strategy for long-term conservation" (Frankel et al. 1995:193). Classification is a necessary premise in conservation planning for ecological units (e.g., communities, ecosystems, or habitats), providing the vocabulary for any discus-

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sion of vegetation. Conservation efforts (DeSimone and Silver 1995) necessitate a classification of coastal sage scrub.

"Coastal sage scrub" is a broad term encompassing a wider variety of floristic composition, structure, and habitat suitability for particular plants and animals than the name implies. Based on 120 sample sites, Kirkpatrick and Hutchinson (1977) identified 11 coastal sage scrub "associations", listing characteristic taxa and describing the physical structure of each one. In addition, they analyzed differences in species composition between two regions (an inland basin and a more coastal area) and concluded that

In fact, the Diegan and Venturan sage appear to intergrade much more gradually than the coastal and inland basin sage distinguished in this study. Thus, at a gross classification level there can be cause for recognizing Venturan, Diegan and Riversidian coastal sage scrub.

Since then, coastal sage scrub classifications have tended to emphasize either (1) Kirkpatrick and Hutchinson's (1977) regional categories, or (2) their floristic assemblages.

Axelrod (1978) retained the name "Riversidian sage scrub" for the interior region and coarsely mapped its distribution. Westman (1983) modified Axelrod's map based on 99 plot sites from the San Francisco Bay area through northern Baja California. Holland (1986) combined Westman's nomenclature with Cheatham and Haller's (1975) geographic subdivisions, but used the spelling 'Riversidean' for the inland basin region. The California Department of Fish and Game's Natural Diversity Data Base (1990) adopted Holland's nomenclature, retaining the original spelling of Riversidian.

Paysen and coworkers (1980) emphasized floristic rather than geographic variation. They recognized eight "series" within their "soft chaparral subformation"; five or six of their series are encompassed within typical descriptions of coastal sage scrub (e.g., Munz 1959), but do not account for the diversity of Kirkpatrick and Hutchinson's (1977) 11 associations. DeSimone and Burk (1992) analyzed 54 plot sites within a small portion of Westman's (1983) Diegan region and identified five "subassociations". Some of these resemble vegetation considered more typical of other geographic areas, indicating that the geographic nomenclature does not adequately represent local variation in coastal sage scrub. Davis and coworkers (1994) identified 13 "species assemblages" based on dominant plants in large (1 km²) mapping units. Sawyer and Keeler-Wolf (1995) recognized 15 coastal sage scrub "series", based on these and other quantitative and qualitative descriptions. The terms "association" (as used by Kirkpatrick and Hutchinson 1977), "subas-

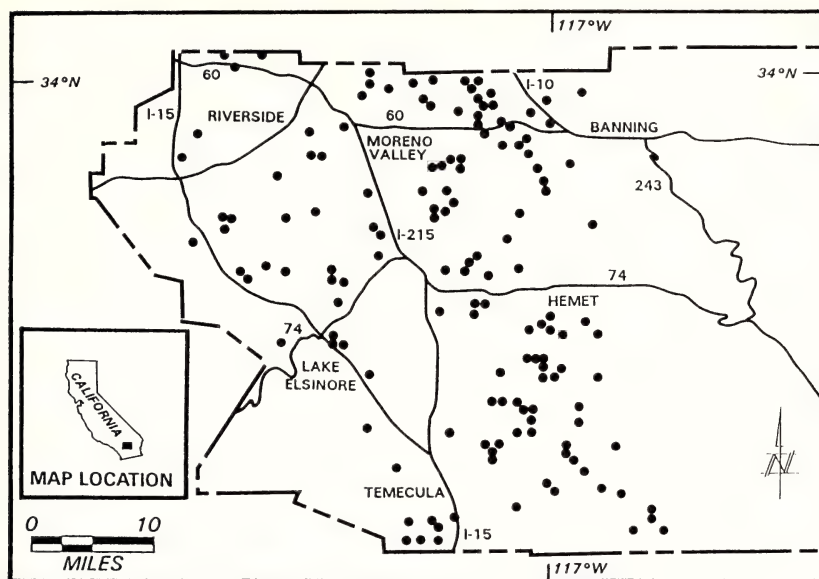


Fig. 1. Study area and sample sites.

sociation" (DeSimone and Burk 1992), and "series" (Paysen et al. 1980; Sawyer and Keeler-Wolf 1995) are roughly equivalent.

DeSimone and Burk (1992) emphasized that more detailed information on variation within geographic regions was needed for conservation planning and Read (1994) stressed the importance of local and regional variation to ecological restoration. In this report, we analyze 181 new plots in western Riverside County and compare them to six assemblages Kirkpatrick and Hutchinson (1977) described in the interior basin. This classification is one component of baseline data intended for use in a regional multiple-species habitat conservation plan (Pacific Southwest Biological Services 1995).

METHODS

Vegetation data were collected at 181 sites within a study area defined by the Riverside County Habitat Consortium (Fig. 1) entirely within Kirkpatrick and Hutchinson's interior basin and Westman's "Riversidian" region). The 540,000 ha study area encompasses about 68,000 ha of coastal sage scrub. It was stratified into 68 whole or partial townships as shown on USGS maps. Total acreage of coastal sage scrub within each township was estimated from aerial photographs (Pacific Southwest Biological Services 1995). Within each township, each $\frac{1}{4}$ section (ca. 65 ha; 160 acres) was numbered. Quarter sections supporting coastal sage scrub in patches

≥ 2 ha were selected randomly to total 12% of the coastal sage scrub within each township. Written permission was requested from the owner(s) of each selected $\frac{1}{4}$ section to survey for biological resources. Permission was granted to sample sites totaling 2700 ha (4%) of mapped coastal sage scrub within the study area. Vegetation data were collected at one to four sites within each $\frac{1}{4}$ section, depending on the extent and distribution of coastal sage scrub. Each selected $\frac{1}{4}$ section was stratified into 16 ha (40 acre) $\frac{1}{16}$ sections and one site was sampled within each $\frac{1}{16}$ section where coastal sage scrub occurred. In addition to collecting vegetation data, each site was surveyed for presence of California gnatcatchers (*Polioptila californica*) (Padley in preparation).

Sample sites were centered near the center of coastal sage scrub patches as identified on aerial photographs prior to visiting the site, except where California gnatcatchers were detected. On these sites, center points were moved to the initial California gnatcatcher position. Location (Township, Range, and $\frac{1}{16}$ section), elevation, slope, and aspect were recorded at each site's center point. Sampling methodology was modified from Evans and Love (1957). Fifty toe-point intercepts were recorded at 2-step (roughly 2 m) intervals along two 100-step transects. Transects originated at the center point, and were directed at 360° and 90° azimuths (north and east, respectively). Shrub cover (species and height) and ground layer (recorded as soil, rock, road, litter, or herbaceous plant category) intercepting a line projected vertically from each toe-point were recorded. If no plant intercepted the vertical line, then no species was recorded. Herbaceous plants were categorized as native or non-native and as forb or grass, but herb species names were not recorded.

Data were analyzed using cluster analysis of cases (an agglomerative program which generates a dendrogram), K-means clustering of cases (a non-hierarchical divisive program), and stepwise discriminant analysis (BMDP Statistical Software 1994). Data were arranged into groups with both cluster programs, using frequency for taxa and herb categories occurring at $\geq 1.0\%$ average frequency throughout the entire data set. These variables were non-native herbs, native herbs, non-native grasses, *Salvia mellifera*, *Encelia farinosa*, *Eriogonum fasciculatum*, *Artemisia californica*, *Adenostoma fasciculatum*, *Lotus scoparius*, *Salvia apiana* frequencies. In cluster analysis of cases, the sum of squares algorithm was used with the centroid clustering method. K-means clustering of cases used unit variance standardized data, set to identify 15 clusters (after preliminary analyses with other values). Results of the two cluster analyses were compared and plots were assigned to groups when both analyses placed them into similar clusters. Plots not clustered similarly by the two programs (68) were excluded from further analysis. Three clusters (totaling 24 plots) were dominated by non-native

TABLE 1. COASTAL SAGE SCRUB SERIES IN WESTERN RIVERSIDE COUNTY, CALIFORNIA.

| Series | Cali- fornia sage- brush | Cali- fornia buck- wheat | CA sage brush- CA buck- wheat | CA sage brush- white sage | Brittle- bush | Black sage | Deer- weed |
|---|-----------------------------------|-----------------------------------|--|---------------------------------------|------------------|---------------|---------------|
| No. of plots | 7 | 8 | 33 | 5 | 14 | 17 | 5 |
| Mean elev. (m) | 410 | 550 | 490 | 380 | 610 | 640 | 580 |
| Mean cover of selected species and categories (%) | | | | | | | |
| Shrubs | 72 | 51 | 45 | 57 | 51 | 71 | 48 |
| Non-native grasses | 3 | 10 | 12 | 2 | 6 | 11 | 16 |
| Non-native herbs | 7 | 6 | 23 | 11 | 16 | 15 | 10 |
| Native herbs | 9 | 14 | 5 | 14 | 4 | 1 | 6 |
| <i>Salvia mellifera</i> | 3 | 0 | 0 | 2 | 2 | 32 | 14 |
| <i>Encelia farinosa</i> | 0 | 0 | 3 | 0 | 41 | 8 | 4 |
| <i>Eriogonum fasciculatum</i> | 11 | 45 | 19 | 2 | 2 | 6 | 7 |
| <i>Artemisia californica</i> | 42 | 0 | 16 | 21 | 5 | 15 | 2 |
| <i>Lotus scoparius</i> | 2 | 3 | 1 | 0 | 0 | 0 | 14 |
| <i>Salvia apiana</i> | 11 | 0 | 1 | 27 | 0 | 0 | 0 |
| Mean height of selected species (m) | | | | | | | |
| <i>Salvia mellifera</i> | 0.3 | — | — | 0.3 | 0.2 | 1.1 | 1.0 |
| <i>Eriogonum fasciculatum</i> | 0.6 | 0.7 | 0.6 | 0.5 | 0.1 | 0.6 | 0.6 |
| <i>Artemisia californica</i> | 0.7 | — | 0.8 | 0.8 | 0.4 | 0.8 | 0.5 |

herbs or grasses with little native shrub frequency. Reviewing the original data revealed that transects at these sites were only partially within coastal sage scrub, crossing into annual grassland over the remainder of their lengths. They were excluded from further analysis. Plot groups characterized by native shrubs were named as series using Sawyer and Keeler-Wolf's (1995) nomenclature or by novel names following Sawyer and Keeler-Wolf's style (i.e., by common names of dominant species).

Series were compared using stepwise discriminant analysis to identify the most useful variables for distinguishing between them, using all available variables. The program was run twice with all series, first using vegetation data (species frequency and height), and then using location (township and range), elevation, slope, and cosine-transformed aspect variables (so that slopes with similar exposure would have similar values).

RESULTS

Seven coastal sage scrub series were identified (Table 1 and Fig. 2). Two series (California sagebrush and California sagebrush-white sage) were classified ambiguously by the two cluster programs but were retained in the classification (identical sets of plots were placed

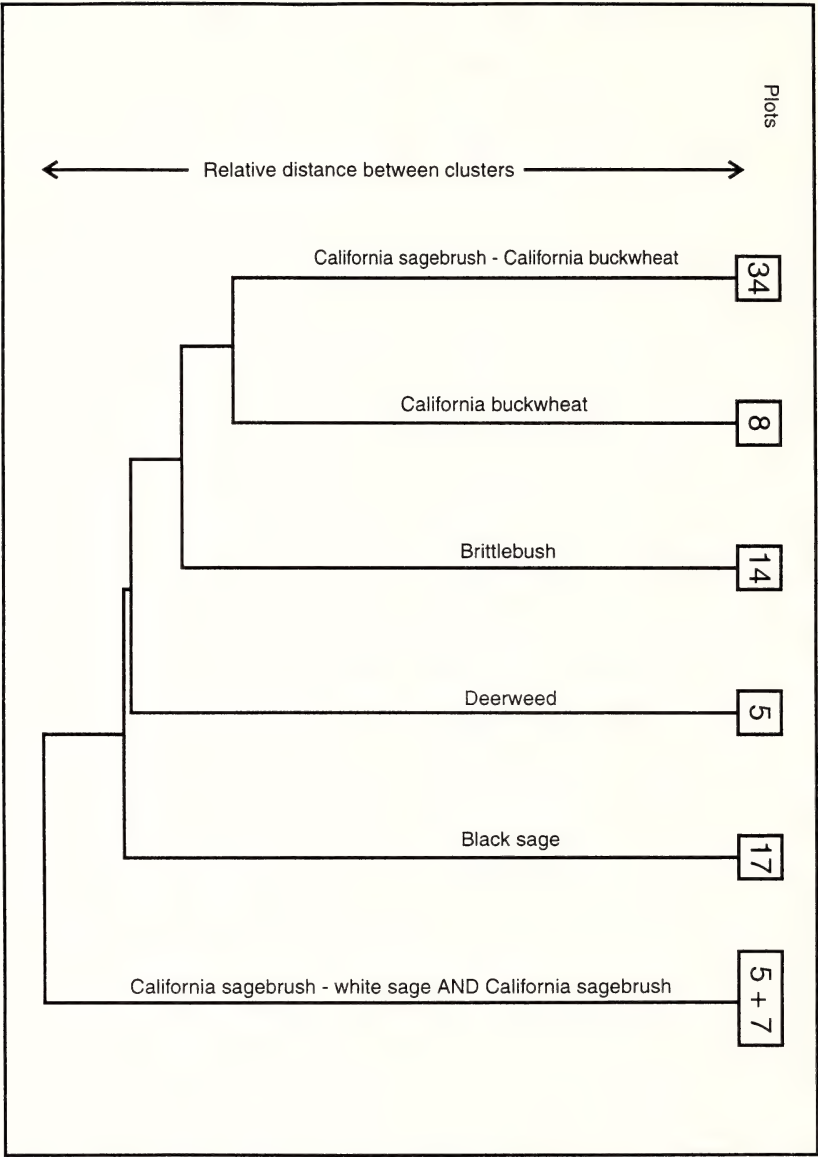


FIG. 2. Results of cluster analyses. Dendrogram indicates results of cluster analysis of cases (vertical scale is proportional to cluster similarity); numerals indicate number of plots shared with K-means cluster analysis results.

into two clusters by K-means clustering of cases, while stepwise clustering of cases combined them).

We classified plots conservatively, assigning them to categories only when both programs clustered them similarly (except as noted above). Eighty nine plots were classified into seven coastal sage scrub series. Twenty four were classified as partially covered by annual grassland and were discarded from the classification. The remaining 68 plots were discarded from the classification due to inconsistent classification or placement into "catch-all" groups.

Stepwise discriminant analysis used 11 vegetation variables to discriminate among the series with 96% overall success. In order of importance, the variables were: *Salvia mellifera* frequency, *Encelia farinosa* frequency, *Salvia apiana* frequency, *Lotus scoparius* frequency, non-native grass frequency, total shrub frequency, *Artemisia californica* frequency, *A. californica* height, *Eriophyllum confertiflorum* frequency, *Eriogonum fasciculatum* height, and non-native herb frequency. Stepwise discriminant analysis had generally poor success discriminating between vegetation series using geographic and physical variables. Township, range, and elevation were the three most useful of these, and were used to classify the black sage and brittlebush series with about 50% success. Other series were classified with much lower success rates.

Kirkpatrick and Hutchinson (1977) named "associations" using scientific names of characteristic species, but Sawyer and Keeler-Wolf (1995) used common names in their nomenclature. We follow Sawyer and Keeler-Wolf's nomenclature and style and provide corresponding scientific names to minimize difficulty in comparing these series to Kirkpatrick and Hutchinson's categories.

The Brittlebush (*Encelia farinosa*) series recognized here matches Sawyer and Keeler-Wolf's Brittlebush series and corresponds well to Kirkpatrick and Hutchinson's *Encelia farinosa*-*Mirabilis laevis* (brittlebush-California wishbone bush) association, though *M. laevis* occurs at low frequency in our data. Our data match Kirkpatrick and Hutchinson's description of physiognomy: this vegetation is open (rarely more than 60% shrub frequency), with lower stature than most other series.

Our Black sage (*Salvia mellifera*) series and California sagebrush (*Artemisia californica*) series correspond respectively to Sawyer and Keeler-Wolf's series of the same name and to Kirkpatrick and Hutchinson's *Salvia mellifera*-*Eriogonum fasciculatum*-*Bromus rubens*, and *Artemisia californica* associations, respectively. Both series are characterized by higher mean total shrub frequency (> 70%) than other series we identify here.

Our analysis splits Kirkpatrick and Hutchinson's *Artemisia californica*-*Eriogonum fasciculatum*-*Salvia apiana* (California sagebrush-California buckwheat-white sage) association into three se-

ries: California buckwheat, California sagebrush–California buckwheat, and California sagebrush–white sage series. They all match Kirkpatrick and Hutchinson's description of open physiognomy dominated by a low shrub layer and with high herb cover. In recognizing California buckwheat and California sagebrush–California buckwheat as separate series, we follow Sawyer and Keeler-Wolf (1995). The California sagebrush–California buckwheat series is the most common and widespread series in our data, occurring almost throughout the geographic range of coastal sage scrub in Riverside County.

Our California sagebrush–white sage series is encompassed by Sawyer and Keeler-Wolf's white sage series. It was combined with the California sagebrush series by one program in our analysis. We chose to recognize it as a separate series because high *Artemisia californica* frequency distinguishes it from Kirkpatrick and Hutchinson's *Artemisia californica*–*Eriogonum fasciculatum*–*Salvia apiana* association, while structure and floristic differences separate it from the California sagebrush series in the K-means cluster analysis. We use the name California sagebrush–white sage series, rather than Sawyer and Keeler-Wolf's White sage series, because average *Artemisia californica* frequency is nearly as high as *Salvia apiana*. We acknowledge that these plots are intermediate between other series and might validly be included within one of the others (i.e., an "association" in Sawyer and Keeler-Wolf's usage).

We identified a deerweed (*Lotus scoparius*) series not described by Kirkpatrick and Hutchinson (1977) or Sawyer and Keeler-Wolf (1995). Most of these plots are in areas where wildfire had occurred a few years previous to sampling. *Lotus scoparius* is often most common in early post-fire stands (Westman 1981; Keeley and Keeley 1984) and we suspect that these plots are transitional to other coastal sage scrub or chaparral series. Kirkpatrick and Hutchinson (1977) did not sample burned sites, so presumably excluded *Lotus scoparius* dominated sites from their data.

DISCUSSION

Two of Kirkpatrick and Hutchinson's (1977) associations were not identified in this analysis. Their *Eriogonum fasciculatum*–*Scrophularia californica*–*Phacelia ramosissima* (California buckwheat–California figwort–perennial phacelia) association could not have been identified by our analysis because native herb species were not recorded during data collection. Kirkpatrick and Hutchinson characterized this association by an abundance of granitic boulders. We noted that high boulder cover was characteristic of plots in the north-eastern study area, and these probably correspond to Kirkpatrick and Hutchinson's *Eriogonum fasciculatum*–*Scrophularia californica*–

Phacelia ramosissima association. These plots generally fell into our California buckwheat series. Kirkpatrick and Hutchinson's *Lepidospartum squamatum*–*Eriodictyon crassifolium*–*Yucca whipplei* (scalebroom–yerba santa–chaparral yucca) association occurs on infrequently flooded alluvial fans and washes (Smith 1980). It was described as Scalebroom series by Sawyer and Keeler-Wolf (1995). Within Kirkpatrick and Hutchinson's (1977) interior basin, most of its extent is in southwestern San Bernardino County, north of our study area.

This analysis largely confirms Kirkpatrick and Hutchinson's (1977) descriptions of coastal sage scrub variation in the inland basin. Principle differences between the two analyses result from differences in sampling technique: they subjectively selected sites to represent all environmental conditions and species assemblages whereas our random selection method may have missed uncommon assemblages. Also, they recorded all species occurring in an indeterminate-sized plot whereas we combined herbaceous species into a few categories and recorded only species occurring at toe-points along structured transects. Similarities to Kirkpatrick and Hutchinson's (1977) results indicate that coastal sage scrub classification is largely repeatable by independent analyses, though differing methodology and interpretation affect the results.

We share DeSimone and Burk's (1992) view that more detailed understanding of local variation within coastal sage scrub is needed for management and conservation planning, and we encourage planning and resource agencies to continue examining this variation. We particularly note that our classification does not consider herbaceous species which account in large part for variation in species richness among coastal sage scrub stands (Westman 1981).

Planners and land managers should not assume that all coastal sage scrub stands will provide suitable habitat for plants and animals whose habitat is described as simply "coastal sage scrub". Floristic and physiognomic differences among coastal sage scrub series offer differing habitat resources to plants and animals. Floristic differences may reflect differing climatic or edaphic conditions, may affect habitat suitability for taxa of special concern, and may support differing assemblages of specialist animal species. Similarly, structural differences will affect understory light availability, cover availability, or animals' ability to detect prey. We recommend conservation planning to encompass as wide a range of conditions as possible, though we recommend against conservation planning for the Deerweed series due to its evident transitional nature.

The series described here successfully classify much of the variation among shrub canopy composition in Riverside County's coastal sage scrub, though gradation among these series and among coastal sage scrub, chaparral, and annual grassland is evident. The large

proportion of unclassified plots is evidence that series recognized here intergrade into one another along continua in structure and/or floristic composition. Many of the unclassified plots seem to be intermediate between series described here or between coastal sage scrub and chaparral (e.g., several unclassified plots include *Adenostoma fasciculatum* or *Ceanothus crassifolius*).

There is wide variation between adjacent coastal sage scrub stands in Orange County (DeSimone and Burk 1992), and similar variation can be seen in Riverside County. If a conservation plan represents series described here in areas large enough to effectively manage edge effects, fire ecology, and California gnatcatcher populations, then we expect that additional canopy diversity represented by our unclassified plots will also be included.

ACKNOWLEDGMENTS

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NOTES

CLARIFICATION OF THREE *CAMISSONIA BOOTHII* SUBSPECIES' DISTRIBUTIONS IN CALIFORNIA.—Scott D. White, Tierra Madre Consultants, 1159 Iowa Ave., Suite E, Riverside, CA 92507 (present address: Psomas and Associates, 3187 Red Hill Ave., Suite 250, Costa Mesa, CA 92626) and Andrew C. Sanders, Herbarium, Department of Botany and Plant Sciences, University of California, Riverside, CA 92521.

Distributions of *Camissonia boothii* (Douglas) Raven ssp. *boothii* and *C. boothii* ssp. *alyssoides* (Hook. & Arn.) Raven have been confused in California floras due to revised taxonomy, a mis-annotated specimen, and insufficient documentation of a southern Mojave Desert population. Munz (1935, *A Manual of Southern California Botany*, Claremont Colleges, Claremont, CA; and 1959, *A California Flora*, University of California Press, Berkeley, CA) reported *C. boothii* ssp. *boothii* in the southern Mojave Desert, but omitted it from his later *Flora of Southern California* (1974, University of California Press, Berkeley, CA), replacing it with *C. boothii* ssp. *alyssoides*. Wagner (1993, *Camissonia*, in Hickman [ed.], *The Jepson Manual*, University of California Press, Berkeley, CA) indicated that neither taxon occurs in the southern Mojave. Skinner and Pavlik (1994, *Inventory of Rare and Endangered Vascular Plants of California*, California Native Plant Society, Sacramento, CA) included both taxa on their watch list, reporting *C. boothii* ssp. *boothii* in Inyo, Mono, and San Bernardino Counties and *C. boothii* ssp. *alyssoides* in Lassen County. We reviewed taxonomic treatments and herbarium specimens at UCR and RSA of these and a third, related subspecies, *C. boothii* ssp. *intermedia*, seeking to clarify their distributions in California. All three subspecies flower late in the growing season and are relatively widespread in the Great Basin, reaching California at the western limits of their ranges (Raven 1969, *Contributions of the U.S. National Herbarium* 37:161–396).

Munz (1928, *Botanical Gazette* 85:233–270) recognized *C. boothii* ssp. *boothii* and *C. boothii* ssp. *alyssoides* as full species, *Oenothera boothii* Dougl. and *O. alyssoides* Hook. & Arn., and retained this nomenclature in his 1959 flora (*op. cit.*). He published a second *Oenothera* treatment in 1965 (*North American Flora Series II*, Part 5:1–231), ranking both taxa as subspecies within *O. boothii*, and describing the closely related *O. boothii* ssp. *intermedia* Munz. This new taxon included a series of specimens with character states intermediate between *O. boothii* and *O. alyssoides*. Raven (*op. cit.*) transferred *O. boothii* to *Camissonia*, retaining these subspecific taxa. Subsequent authors (Munz 1968, *Supplement to A California Flora*, University of California Press, Berkeley, CA; Munz 1974, *op. cit.*; Wagner *op. cit.*) have followed Raven's nomenclature.

Munz (1935, *op. cit.*) first reported *Camissonia boothii* ssp. *boothii* (as *Oenothera boothii*) occurring in the southern Mojave Desert, as "rare in So. Calif. (Hesperia region on Mojave Desert)." The only specimen housed locally that would have supported his report was collected at Victorville in 1916 (*Frank Pierson* 792 RSA), though Raven (*op. cit.*) cited two specimens in other collections (*S. B. & W. F. Parish* 1504 DS, F, GH; and *Abrams* 2166 no herbarium cited) from the same area. Pierson's specimen was annotated by Raven in 1966–1967 as *C. boothii* ssp. *alyssoides* but was cited in his monograph (*op. cit.*) as *C. boothii* ssp. *boothii*. Curiously, he did not map either taxon in the southern Mojave Desert (*op. cit.*:359). Munz, evidently working from the annotated RSA collection (i.e., *Pierson* 792) rather than citations in Raven's monograph, reported *C. boothii* ssp. *alyssoides* rather than *C. boothii* ssp. *boothii* in his second southern California flora (1974 *op. cit.*).

Camissonia boothii ssp. *boothii* and *C. boothii* ssp. *alyssoides* are distinguished by pubescence characters and dimorphic vs. monomorphic seeds (Raven *op. cit.*; Wagner

1993 *op. cit.*). *Camissonia boothii* ssp. *intermedia* and *C. boothii* ssp. *boothii* share these character states; they are distinguished by stature, leaf shape, and leaf margin characters. Wagner (*op. cit.*) noted that *C. boothii* ssp. *boothii*'s (mature) fruits are wider (1.4–2 mm) than those of the other two subspecies (1–1.4 mm), though this character does not appear in his key. We also note that *C. boothii* ssp. *boothii* capsules are generally shorter (ca. 10–14 mm) and less twisted (sickle-shaped, ascending and arching outward, bent twice at most) whereas *C. boothii* ssp. *alyssooides* and *C. boothii* ssp. *intermedia* capsules are longer (≥ 14 mm), usually serpentine, bent twice or more, not usually ascending, and more commonly bending downward (illustrated for *Oenothera alyssoides* in Abrams 1951, *Illustrated Flora of the Pacific States III*, Stanford University Press, Stanford, CA:203).

Pierson's Victorville specimen keys to *C. boothii* ssp. *boothii*, though its capsules are longer and more twisted than typical, resembling those of *C. boothii* ssp. *intermedia* (the southern Mojave *C. boothii* ssp. *boothii* population is illustrated as *Oenothera boothii* in Jaeger 1941, *Desert Wild Flowers*, Stanford University Press, Stanford, CA:170). Three additional southern Mojave Desert specimens at UCR are similar in all character states, including capsule shape: *Ken Kroesen s.n.* (11 Aug. 1981, "southern Mojave Desert, collected along the Mojave River 1/2 mile upstream from Oro Grande, soil very sandy"); *Stephen Myers s.n.* (26 Sept. 1989, "Apple Valley, Yucca Loma Rd. at the Mojave River, 2800 ft. elev."); and *Stephen Myers 91-50* (27 Aug. 1991, "at the foot of the San Bernardino Mts., near Hesperia, Mojave River 1 mi. N. of Mojave Forks Dam"). These collections certainly represent the populations Munz reported in 1935 (*op. cit.*). One additional specimen, *R. Hoffman 576 POM*, collected near Little Lake in Inyo Co., has capsules much like the southern Mojave Desert plants.

The southern California locations are far distant from the remainder of *C. boothii* ssp. *boothii*'s reported distribution and were erroneously excluded from the distribution as described in *The Jepson Manual* (Wagner *op. cit.*). The only other California *C. boothii* ssp. *boothii* we have seen were several specimens collected near Mono Lake (ca. 370 km north) and Hoffman's specimen near Little Lake, ca. 160 km north, annotated by Raven as "out of normal range" and cited in his monograph). We note that *C. boothii* ssp. *boothii* from the Mono Lake region are much more densely pubescent than those collected elsewhere.

Outside California, the nearest collections are from Mojave Co., Arizona, ca. 380 km east (*Cooper s.n.* GH, cited by Raven [*op. cit.*]; Phillips et al. 1987, Annotated checklist of Vascular Plants of Grand Canyon National Park, Grand Canyon Natural History Association [no specimen citation], and *Cottam 13348 RSA*). Cottam's is the only Arizona specimen we have seen; its capsules are typical of *C. boothii* ssp. *boothii*. Like the southern Mojave Desert plants, the Arizona location is far distant from the remainder of the taxon's Great Basin distribution.

Camissonia boothii ssp. *intermedia* overlaps in all character states except seed dimorphism with the two other subspecies discussed here (Raven *op. cit.*), and we find it most similar to *C. boothii* ssp. *boothii*. We examined several Nevada specimens labeled *C. boothii* ssp. *intermedia*, including some determined by Raven, that key to *C. boothii* ssp. *boothii* in Raven's (*op. cit.*) and Wagner's (*op. cit.*) treatments. One of the Nevada specimens, *J. Morefield 4647 RSA*, was collected in the White Mountains, (Esmeralda Co.), suggesting that *C. boothii* ssp. *boothii* may also occur in the California portion of the range, though it has not been documented there. Other Nevada specimens we examined strongly resemble *C. boothii* ssp. *boothii*, with only their low stature supporting determination as *C. boothii* ssp. *intermedia*. On most of these plants, the fruit characters described above would argue further for their determination as *C. boothii* ssp. *boothii*. Plant stature is a weak character since young plants and those on poor sites are likely to be small. Consistent with Wagner (*op. cit.*), all California *C. boothii* ssp. *intermedia* specimens we have seen are from mountains of the northeastern Mojave Desert, White-Inyo Mountains, and Owens Valley.

Munz (1959 *op. cit.*) described the California range of *Oenothera alyssooides* Hook. & Arn. var. *villosa* S. Watson as "Kingston and Panamint mts. in Inyo Co. to Lassen Co.," and in 1974 (*op. cit.*) reported it from "the Victorville region." We have seen no *C. boothii* ssp. *alyssooides* material from the desert mountains; plants from that region are now placed in *Camissonia boothii* ssp. *intermedia*. Munz's report of *C. boothii* ssp. *alyssooides* near Victorville was evidently based only on the mis-annotated Pierson specimen. The only California *C. boothii* ssp. *alyssooides* material we have seen was collected from the Modoc Plateau: two specimens from Lassen County (*M. E. Jones s.n.* RSA [23 June 1897]; *P. A. Munz 11869* RSA) and one from Modoc County (*B. Bartholomew & B. Anderson 4812* RSA). Thus, we concur with Wagner's (1993 *op. cit.*) description of *C. boothii* ssp. *alyssooides*'s California distribution being limited to the Modoc Plateau.

All three subspecies have rarely been collected in California. The Modoc Plateau *Camissonia boothii* ssp. *alyssooides* occurrences, Inyo County and desert mountain occurrences of *C. boothii* ssp. *intermedia*, and Mono Lake *C. boothii* ssp. *boothii* occurrences are all within narrowly defined geographic regions at the western margins of their respective wider distributions in the Great Basin. The southern Mojave Desert plants may be a unique long-disjunct population, or may occur infrequently farther north as suggested by the Little Lake specimen. We conclude that they are best ascribed to *C. boothii* ssp. *boothii*, but their capsule morphology suggests introgression with *C. boothii* ssp. *intermedia*. Clearly, they are not *C. boothii* ssp. *alyssooides*. Twenty six years ago, Raven (*op. cit.*) wrote that

Plants of this sort have not been collected in these areas for nearly 40 years. The relationship of these populations to other subspecies should be investigated when additional material becomes available.

We agree, and particularly recommend late-season searches of sandy washes on desert-facing slopes of the southern Sierra Nevada, Tehachapi, and San Gabriel Mountains to further define their distribution.

PHYTOLACCA ICOSANDRA L. (PHYTOLACCACEAE): NEW TO THE CONTINENTAL UNITED STATES.—Victor W. Steinmann, Rancho Santa Ana Botanic Garden, 1500 N. College Ave., Claremont, California 91711.

Phytolacca icosandra L. [= *Phytolacca octandra* L.] (Phytolaccaceae) is a ruderal species previously known from northern México to northern South America; it has also become widely naturalized in the Old World tropics (Nowicke, *Annals of the Missouri Botanical Garden* 55:294–364, 1968). Like other members of the genus *Phytolacca*, it is most frequently encountered in disturbed sites. In December of 1990 a collection of *P. icosandra* was made in the Santa Catalina Mountains of Pima County, Arizona. The plants were restricted to recently burned chaparral in a remote area of Romero Canyon at 1480 to 1800 meters. An examination of specimens at the University of Arizona Herbarium (ARIZ) revealed two misidentified collections made over 50 years ago from the Chiricahua Mountains of Cochise County, Arizona, that are also of this species (see cited specimens). While *P. icosandra* is introduced in many areas, this does not seem to be the case in Arizona. Instead, it appears to be a rare native taxon.

Plants of this species are short-lived perennials characteristic of early successional areas (Floyd, *Australian Forestry* 39:210–220, 1976). Scarification or high temperature is necessary to break the seed coat and allow permeability to water and/or gas. Floyd (*Australian Journal of Botany* 14:143–156, 1966) found that *Phytolacca* seeds had very poor germination unless heated but were able to remain dormant in the soil until this takes place. In a study of a closely related species, *P. rivinoides* Kunth &

Bouché, in Costa Rica, the seeds were found to remain dormant in the soil until a gap was formed in the canopy (Murray, *Ecological Monographs* 58(4):271–298, 1988). In addition, an experiment with *P. americana* L., another closely related taxon, showed that seeds buried in the soil for 39 years had a germination rate of 86%; this was 12% higher than seeds buried for a single year (Toole, *Journal Agricultural Research* 72:201–210, 1946).

It is well known that chaparral is a fire-dependent plant community. In southeastern Arizona this community is mostly confined to the Coronado National Forest, a series of disjunct, sky-island forests surrounded by desert and grassland habitats. In the Santa Catalina Mountains, lightning-initiated fires are frequent during the summer rainy season, and such fires are recognized as part of the natural environment (Whittaker & Niering, *Ecology* 46:429–452, 1965).

The Santa Catalina Mountains, located north of the city of Tucson, are heavily used for recreation. However, the ruggedness of the terrain, characterized by rock escarpments and steep slopes, makes many areas accessible only with great difficulty. Although crossed with trails, the range has few roads and there remain large expanses of isolated, pristine areas. It was in such an area that *P. icosandra* was encountered. The population consisted of about two dozen individuals restricted to a single ridge 300–620 m above the nearest trail and more than 4 km (airline) from the nearest road.

Phytolacca berries are relished by birds, and whether southeastern Arizona's isolated outposts are the result of bird dispersal from populations to the south or whether they represent relicts of a once more northerly distribution is uncertain. In my opinion, human introduction can be ruled out because of the isolation of the plants in the Santa Catalina Mountains, and because of the specimens collected more than 50 years ago from a population disjunct more than 100 km in the Chiricahua Mountains. The otherwise nearest record of this species is from Sonora, México, approximately 100 km south of the Arizona border (see cited specimens), and it is widespread in Sonora and much of México. The fourteen dominant plants in the chaparral of the Santa Catalina Mountains are all northern extensions of predominantly Mexican species (Shreve, *Carnegie Institute Publication* 217:1–112, 1915). *Phytolacca icosandra* is surely not out-of-place in this community.

SPECIMENS CITED

USA, Arizona, Cochise County, Chiricahua National Monument, Bonita Canyon, 12 Aug 1939, *Clark 8569* (ARIZ); Cochise County, Chiricahua Mountains, Chiricahua National Monument, 1850 m, 19 Oct 1940, *Darrow s.n.* (ARIZ); Pima County, Santa Catalina Mountains, Romero Canyon, burned area, 1525 m, 15 Dec 1990, *Steinmann 229* (ARIZ). MEXICO, Sonora, region of the Río Bavispe, Rancho Cruz Díaz, pine zone, 7 Aug 1940, *Phillips 427* (GH).

I am indebted to R.S. Felger, A. Harlan, P.S. Martin, L.A. McDade, T.S. Ross, T.R. Van Devender, and R.K. Wilson who all provided numerous useful comments. For access to their collections I thank the curators and staffs at ARIZ and GH.

ABSENCE OF NASCENT INFLORESCENCES IN *ARCTOSTAPHYLOS PRINGLEI*.—Jon E. Keeley, Department of Biology, Occidental College, Los Angeles, CA 90041.

One of the defining characteristics of *Arctostaphylos* (manzanitas) is the production of inflorescences in the spring or summer, six to eight months prior to flowering (Fig. 1). Jepson (*Erythraea* 8:97–99, 1938) was the first to point out this phenomenon and he coined the term “embryonic panicles” to describe this dormant stage in flowering. Later students of *Arctostaphylos* have replaced this with the term “nascent” inflorescence; defined as inflorescences “developing or coming into existence.”

Jepson was particularly taken with these structures because he noted that, although

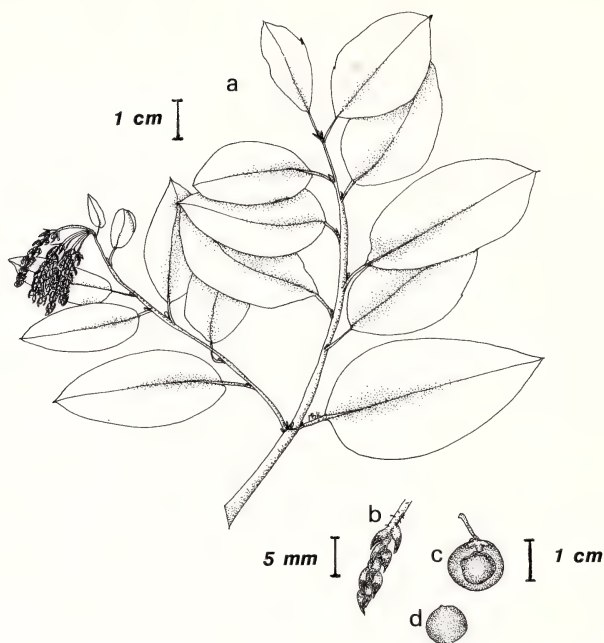


FIG. 1. a. Branchlet with dormant nascent inflorescence as it appears for 6–9 months of the year in *Arctostaphylos* species, except *A. pringlei*. b. Single branch of nascent inflorescence. c. Fruit (with solid endocarp, d) which is often present at the same time as nascent inflorescences (*Arctostaphylos rainbowensis* illustration is from Madroño 41:1–12).

flowering panicles were remarkably similar among species, “these embryonic panicles were found to be strikingly unlike.” He noted numerous examples in *Arctostaphylos* where these structures were of great taxonomic importance and concluded that “it now seems probable that in all species of *Arctostaphylos* the embryonic panicles will be found to exhibit characteristics which are of importance taxonomically.” Jepson’s prediction has held up and today these nascent inflorescences are key characters in the taxonomy of the group, which comprises 62 recognized species, and many more subspecific forms.

I report here, after having observed over 60 species of *Arctostaphylos* in the field, that nascent inflorescences are practically ubiquitous in the genus, save one species, *A. pringlei* Parry. This is a diploid species ($n=13$, J. Keeley), widespread throughout the southwest. The conclusion of lack of nascent inflorescences in *A. pringlei* is based on numerous observations of this species in late summer throughout much of its range from Baja California and southern California. In all cases, plants lacked nascent inflorescences. This phenological pattern is apparently typical throughout the range as data from Arizona populations of *A. pringlei* also indicate a lack of inflorescence development until immediately prior to flowering (A.D.S. Harlan, Ph.D. dissertation, University of Arizona, Tucson, 1977).

In addition to these observations, more detailed field study was made on two populations of this species from June 1992 through April 1993. One of the two populations was near Angelus Oaks (1725 m) in the San Bernardino Mtns (San Bernardino Co.) and the other at 2000 m in the Santa Rosa Mtns (Riverside Co.).

Populations were visited at irregular intervals up through the end of autumn (December 1992). During this period no nascent inflorescences were produced. In late autumn the axillary buds at the tips of new growth, which will give rise to flowering panicles the following spring, were swollen. These buds appeared to be entirely vegetative as hand sections of these buds, examined under 30 \times magnification, did not reveal any floral structures.

Populations were visited again in April 1993 and shrubs were in the initial stages of flowering. On the same shrub all stages of inflorescence development were evident, from dormant apical and axillary buds just breaking dormancy, to barely visible embryonic panicles and all stages of inflorescence development through to flowering. These flowering panicles arose from meristems on the old growth from the previous year, as is the case in other *Arctostaphylos* species.

Clearly, *A. pringlei* is set apart from the rest of *Arctostaphylos* in the lack of nascent inflorescence production. Outside the genus clearly evident nascent inflorescences are of limited distribution in the Ericaceae, although early floral development in the growing season prior to flowering is apparently widespread in the family (H. P. Bell and J. Burchill, Canadian Journal of Botany 33:547–561, 1955). *Arctostaphylos* is the largest of six genera within the subfamily Arbutioideae. The two most closely related genera, *Ornithostaphylos* and *Xylococcus* (indeed, older taxonomic treatments subsumed them in *Arctostaphylos*), produce nascent inflorescences in the year prior to flowering, as in *Arctostaphylos* (minus *A. pringlei*). *Comarostaphylis* and *Arctous* lack nascent inflorescences, as do North American *Arbutus* species; however the European *Arbutus unedo* does produce *Arctostaphylos*-like nascents (Keeley unpublished field and herbarium observations).

This profound phenological difference between *A. pringlei* and the rest of the genus sets this species apart and is consistent with other attributes. For example, Wells (Four Seasons 9(2):64–69, 1992) was so impressed with the uniqueness of *A. pringlei* that he erected a third section within subgenus *Arctostaphylos* for this species alone. The section, *Pictobracteata* Wells, is distinguished by large membranous floral bracts, and the phenological observations reported here support its distinction from the rest of the genus.

A NEW CHROMOSOME NUMBER FOR *SAXIFRAGA CALIFORNICA* (SAXIFRAGACEAE) WITH IMPLICATIONS FOR ITS RELATIONSHIPS.—John F. Gaskin and Patrick E. Elvander, Department of Biology, University of California, Santa Cruz, CA 95064.

Saxifraga californica Greene and *Saxifraga fallax* Greene (Saxifragaceae) were treated as separate species by Munz (*A California Flora*, University of California Press, 1965). Elvander (Systematic Botany Monographs, 3:1–44, 1984) combined the two taxa into one species, *S. californica*. A study exploring the justification of Elvander's incorporation of these two species into one found no consistent or significant morphological differences between herbarium specimens (UC, JEPS) which were previously classified as *S. fallax* and herbarium specimens which were always classified as *S. californica*. During the study, buds were collected from a population (Gaskin 003, UCSC) that had previously been identified as *S. fallax* from the Sierra foothills and one (Gaskin 002, UCSC) that had always been identified as *S. californica* from the Coast Range of California. A consistent haploid chromosome number of $n=10$ was found for these specimens. This is the first chromosome number report for this species. It gives new insight into the relationship of *S. californica* to other members of the genus and supports the morphological conclusion that there is only one species.

The relationships of *S. californica* to other species in the section *Boraphila* series *Integrifoliae* have been difficult to determine since *S. californica* has morphological characters representative of both the *S. rhomboidea* (Greene) complex, representing

series *Nivali-virginiensis*, and the *S. integrifolia* (W.J. Hooker) complex, representing series *Integrifoliae* (Elvander 1984). *Saxifraga californica* is the only species studied in *Integrifoliae* with the putatively primitive characteristics of having anthers and stigmas maturing simultaneously and being self-incompatible. Other related species are protandrous and self-compatible (Elvander 1984). Engler and Irmscher [Das Pflanzenreich IV. 117 (Heft 67), Leipzig, 1916] placed *S. californica* in series *Nivali-virginienses* due to its prominently serrate leaves and reportedly superior ovaries. Elvander (1984) indicated that ovary position was actually inferior prior to fruit maturation, and on this basis, placed *S. californica* into series *Integrifoliae*, near the *S. rhomboidea* and *S. integrifolia* species complexes. Its ultimate affinities remained uncertain.

The new chromosome number suggests that *S. californica* is most closely related to a hypothetical "protointegrifolia" ancestral group (Elvander 1984), which is based on $x = 10$. In overall morphology, habit, and habitat, *S. californica* most closely resembles *S. nidifica* var. *claytoniifolia* (Canby ex Small) Elvander of the *S. integrifolia* complex, which has reported chromosome numbers of $n=10$ and 19 (Elvander 1984). The leaf morphology of *S. californica* suggests a relationship with the *S. rhomboidea* complex, which has reported chromosome numbers of $n=10, 19, 28$, and 29 (Elvander 1984). Further systematic work is needed to resolve the relationships of *S. californica*.

REVIEW

The Flora of Guadalupe Island, Mexico. By REID MORAN. Memoirs of the California Academy of Sciences. No. 19, 1996. 190 pp. Hardcover, 13 color photos, 76 b/w photos, \$40.00 (from publisher). ISBN 0-940228-40-8.

Guadalupe Island is a volcanic oceanic island 260 km west of the Baja California peninsula in Mexico and 400 km south-southwest of San Diego, California. The island is an outlying component of the California Floristic Province that has been ravaged by a plague of feral goats that has devoured much of the island and changed its very image by eradicating native plant species, causing extensive soil erosion, and drying springs by killing trees responsible for increasing the water content on the island by fog drip. With this book, Moran documents the sad and ever too common story of an island ecosystem broken by the introduction of outside species. In this case, the pestilence of goats and weedy non-native (mostly European) plant species and their degrading effects.

This book exhibits Dr. Moran's botanical expertise and the value of his meticulous work, plus it reveals his first-hand knowledge from numerous trips in a 40-year history with Guadalupe Island. It is well-formatted and indexed so that information can be found quickly and easily.

The contents of the book include a physical description of the island; history; discussion of native and foreign plants; vegetation, with special reference to floristic affinities and extinct plants; goat impacts; plant collectors; and a complete catalogue of the vascular flora containing observations, discussions, and distributional ranges for each taxon. It should be noted that the book does not have any dichotomous keys for plant identification.

The floristic analysis provides information on 216 species. Probably 171 species should be considered native, and of these taxa 34 (21.8%) are endemic, including two monotypic genera. It is known that at least 30 species that once grew on the island are now extinct; five of these were endemic. However, this number is most likely an underestimation, since it is not possible to know what plants occurred on the island before the arrival of goats sometime before 1859. This analysis of the native flora confirms its major affinities to the north with the Channel Islands off southern California showing a 73.1% similarity comparison.

The book supplies invaluable and detailed notes on the various plant collectors who visited the island, what they found, collected, contributed to our knowledge of the flora, and where their botanical collections are filed. It also provides an interesting discussion about the problems encountered during the categorization of native and non-native plants on an oceanic island that began as bare volcanic rock.

It is very difficult to find much fault with this book. Only a couple of minor typographical errors were noted. Most of the photos were black and white, and as a result some of the landscape shots are lacking much contrast and would be better in color. However, this secondary detraction has nothing to do with the work itself and is probably a product of the high cost of printing color photos.

Outside of its pure scientific value, I hope that this book impacts public awareness and stimulates changes in Mexican land policies regarding Guadalupe Island. It behooves all interested parties to heed the author's recommendation to remove all goats from the island in an attempt to reverse the degradation processes and foster a renewal of natural vegetation. Although it may be too late for some species, a conservation endeavor may at least serve as a manner of polishing this island jewel, one of Mexico's national treasures.

Dr. Moran's book is an excellent addition to anyone's botanical library. He has

compiled his floristic experience, long-term observations, and detailed literature studies on Guadalupe Island and adjacent areas to synthesize a well-written and informative flora which can serve as a an exemplar for future floristic research.

—JON P. REBMAN, San Diego Natural History Museum, P.O. Box 1390, San Diego, CA 92112.

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NOTES ON THE TAXONOMY AND DISTRIBUTION OF CALIFORNIA *SALIX*

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ABSTRACT

There are 29 taxa of native *Salix* and two species of naturalized tree willows in California. Notes on the taxonomy and distribution of these willows, made during the study of *Salix* for *The Jepson Manual*, are presented. The data included are synonymy, a statement of geographical distribution, comments on taxonomic problems and hybridization, and dot distribution maps. A key is presented to the naturalized species, hybrids, and cultivars. The greatest biodiversity of *Salix* is in the Sierra Nevada Region and the lowest in the Desert Region.

During the preparation of a treatment of *Salix* for *The Jepson Manual* (Hickman 1993) notes were made on taxonomic problems, synonymy, and distribution that could not be included in the flora. The purpose of publishing this information is to bring attention to taxonomic problems and encourage their investigation. It is also an opportunity to present current thinking on the taxonomy of some taxa and to make distribution maps available. This is the first time that California *Salix* have been mapped, other than the tree willows (Little 1971, 1976).

MATERIALS AND METHODS

Taxonomic and distributional data were obtained from the study of herbarium specimens in CAN, CAS, DS, F, JEPS, MO, NA, NY, POM, RSA, SFV, UC, US, and WTU (abbreviations after Holmgren et al. 1990). Locality data for many specimens were recorded. Latitude and longitude, when not given on the labels, were determined using the *Geographical Names Information System California*, 1991. U. S. Geological Survey, Reston, VA. Mapping coordinates were entered into a dBASE file. Distribution maps were plotted using the database manager inFOCUS (Earth and Ocean Research Ltd., Dartmouth, Nova Scotia) and QUIKMap (AXYS Software Ltd., Sidney, British Columbia) as described by Haber (1993). Some range details may be lacking because mapping coordinates could not be found for all specimens; additions and corrections would be welcome.

The geographical occurrence of taxa in California was determined using an overlay of the geographic subdivisions of California (Hickman 1993). For most species there are minor differences in geo-

graphical occurrence as given in *The Jepson Manual* (Hickman 1993). This was because the original ranges were based on lists of localities and not on actual maps.

The synonymy accounts for names used in California floras (Bebb 1880; Hickman 1993; Jepson 1923; Mason 1957; Munz 1959, 1968, 1974), the flora of the Pacific Northwest (Hitchcock et al. 1964), and recent taxonomic literature. Full citations are given only for accepted names and their basionyms. Nomenclatural changes from *The Jepson Manual* treatment are indicated by cross-references in the taxonomic section.

TAXONOMY AND DISTRIBUTION OF NATIVE WILLOWS

Salix arctica sensu *The Jepson Manual* = *S. petrophila*.

1. *Salix bebbiana* Sarg. Gard. & For. 8:463. 1895

Modoc Plateau. Known only from south of Lower Klamath Lake, Siskiyou Co., and the southeast shore of Modoc Lake, Modoc Co. Map 1. Newfoundland to Alaska southward to Maryland and South Dakota, and, in the Cordillera, to Arizona and New Mexico; Eurasian.

2. *Salix boothii* Dorn, Canad. J. Bot. 53:1505. 1975

S. pseudocordata auctt. misapplied not (Andersson) Rydb.

Klamath Ranges, High Cascade Ranges, North and Central High Sierra Nevada, Modoc Plateau (Warner Mts.), East of Sierra Nevada (White Mts., Fishlake Valley drainage). Map 2. British Columbia and Alberta southward to Arizona and New Mexico.

3. *Salix brachycarpa* Nutt. N. Am. Sylva 1:69. 1842. var. *brachycarpa*

Central High Sierra Nevada. Known only as a disjunct population in Convict Creek Basin, Mono Co. Map 1. Alaska to Quebec southward in the Cordillera to California and New Mexico.

4. *Salix breweri* Bebb in S. Watson, Bot. Calif. 2:88. 1879

Outer and Inner North Coast Ranges, San Francisco Bay Area, Outer and Inner South Coast Ranges. Map 3. Endemic to California. See *S. delnortensis*.

5. *Salix delnortensis* C. K. Schneider, J. Arnold. Arbor. 1:96. 1919

S. breweri Bebb var. *delnortensis* (C. K. Schneider) Jeps.

Klamath Ranges. Known only from Del Norte Co, CA, and Josephine Co., OR. The California population is restricted to the banks of the Smith River. Map 4. Endemic to California and Oregon.

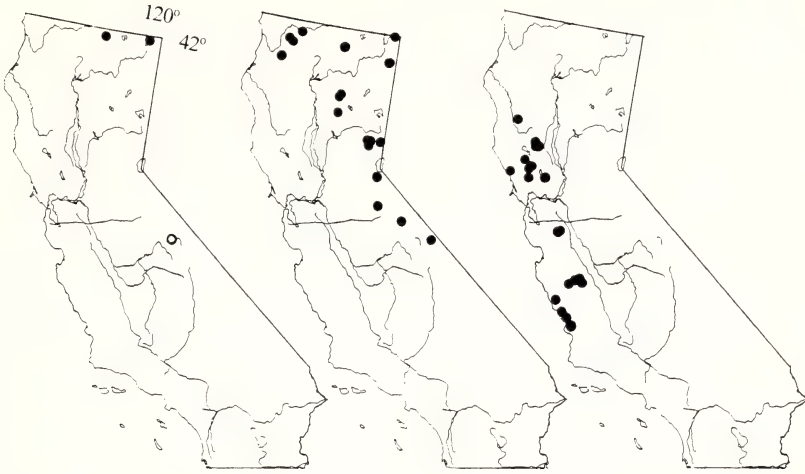


Fig. 1.
● *Salix bebbiana*
○ *Salix brachycarpa*

Fig. 2.
● *Salix boothii*

Fig. 3.
● *Salix breweri*

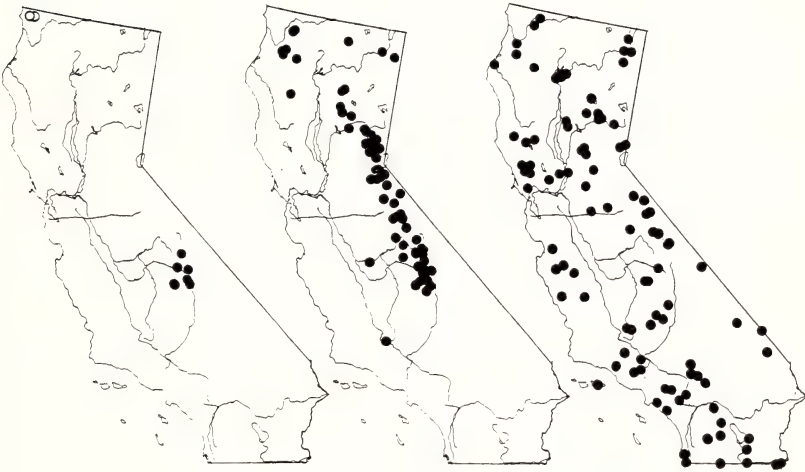


Fig. 4.
○ *Salix delnortensis*
● *Salix drummondiana*

Fig. 5.
● *Salix eastwoodiae*

Fig. 6.
● *Salix exigua*

Maps 1-6.

The lack of variation in herbarium specimens of *S. delnortensis* suggests that it is a single, interbreeding population. This species has usually been compared with *S. breweri* (Schneider 1919:97) and is sometimes treated as a variety of that species (Jepson 1923). In a phenetic study (Argus 1997), the overall morphology of *S. delnortensis* placed it nearest to *S. jepsonii* and *S. sitchensis*, followed by *S. drummondiana*, *S. riskindii* M. C. Johnston, and *S. breweri*. Based on these data, it was included in *S. sect. Sitchenses* (Bebb) C. K. Schneider, along with *S. sitchensis* and *S. jepsonii*. *Salix breweri* was placed in the closely related, monotypic section, *S. sect. Breweri* C. K. Schneider. A case could be made, however, for placing them all in the same section. The question of the relationship of these species could well be studied using molecular techniques.

Dorn's (1976) hypothesis that *S. delnortensis* is a hybrid between *S. lasiolepis* and *S. sitchensis* is not supported by my studies but it should be tested further.

6. *Salix drummondiana* J. Barratt ex Hook. Fl. bor.-am. 2:144. 1838

S. drummondiana var. *subcoerulea* (Piper) C. R. Ball; *S. subcoerulea* Piper

Southern High Sierra Nevada (Kings Canyon and Sequoia National Parks and Inyo National Forest). Map 4. Western North America from the Yukon and Northwest territories southward in the Cordillera to California and New Mexico.

A putative hybrid, *S. drummondiana* \times *S. jepsonii*, with long stigmas, dark brown floral bracts, and no seed development, was collected at Alta Meadows, Sequoia National Park, Tulare Co. (Parks 1042 NA)

7. *Salix eastwoodiae* Cockerell ex A.A. Heller, Cat. N. Am. Pl. ed. 3 89. 1910

S. californica Bebb; *S. commutata* auctt. not Bebb; *S. commutata* var. *denudata* auctt. not Bebb

Klamath Ranges, High North Coast Ranges, High Cascade Range, San Joaquin Valley (high elevations in Fresno and Kern cos.), Modoc Plateau (Warner Mts.), East of Sierra Nevada. Map 5. Washington and Montana southward to California and Colorado.

Authors have reported *S. commutata* from Trinity, Siskiyou, and Modoc cos. (Jepson 1923, Mason 1957, Munz 1959), but it was not included in *The Jepson Manual* (Argus 1993). Specimens from Modoc Co. were reidentified as *S. boothii*, and specimens from Trinity and Siskiyou cos. were reidentified as *S. eastwoodiae*. Dorn (1975) also recognized only *S. eastwoodiae* in California. He separated *S. eastwoodiae* and *S. commutata* by ovary indumentum (sericeous vs. glabrous, respectively) and chromosome number (tetraploid vs. dip-

loid, respectively). He further noted that *S. eastwoodiae* had proximal leaves (and leaves on flowering branchlets) mostly narrower and prominently glandular-margined. My observations show that these species are often the same in these characters and are, in reality, very difficult to separate. Furthermore, the single specimen of *S. eastwoodiae*, on which the chromosome number difference is based (Dorn 1866, RM, CAN), is an unusual specimen in which the proximal leaves, and leaves of the flowering branchlets, lack glandular margins. The reported difference in capsule indumentum (Dorn 1975) also is variable. Collections of *S. eastwoodiae* from Green Lake, Bishop Creek Region, Inyo Co. (Leschke 6 Aug 1944, and Raven & Stebbins 248 CU) include plants with both sericeous and glabrous ovaries. Further study is needed to determine if *S. commutata* is separable from *S. eastwoodiae* and if it occurs in northern California.

Putative hybrids *S. eastwoodiae* \times *S. lemmonii* have been seen from Minear, Tehama Co., and Sulphur Works, Lassen Co.

8. *Salix exigua* Nutt. N. Amer. Sylv. 1:75. 1842

S. argophylla Nutt.; *S. exigua* var. *parishiana* (Rowlee) Jeps.; *S. hindsiana* Benth.; *S. hindsiana* var. *leucodendroides* (Rowlee) C. R. Ball; *S. hindsiana* var. *parishiana* (Rowlee) C. R. Ball; *S. longifolia* var. *argophylla* Andersson, *S. longifolia* var. *exigua* (Nutt.) Bebb; *S. sessilifolia* var. *hindsiana* (Benth.) Andersson; *S. sessilifolia* var. *leucodendroides* (Rowlee) C. K. Schneider

Throughout California but absent from the Tehachapi Mts., the Central Coast, and the White and Inyo Mts. Gaps occur in the Outer North Coast Ranges, High Sierra Nevada, San Joaquin Valley, South Coast Ranges, central Mojave Desert, and northeastern Sonoran Desert. Map 6. British Columbia to Saskatchewan southward to northern Mexico.

Plants of *S. exigua* with spreading hairs on leaves and branchlets; long (0.6–1 mm) slender stigmas; and more or less entire leaves are often referred to *S. hindsiana* (Brunsfield et al. 1992; Munz 1959, 1974). Plants exhibiting these characters occur throughout California. This taxon has not been recognized (Argus 1993) because its characters are so variable that many specimens could not be named with confidence. The problem is compounded, nomenclaturally, because the type of *S. hindsiana* does not have long stigmas, they are only 0.25–0.4 mm long, or leaves with distinctly spreading hairs. The variant named *S. hindsiana* may reflect ancient hybridization and introgression between *S. exigua* and *S. sessilifolia* as asserted by Brunsfield et al. (1992) but I have not been able, based on morphology or geography, to separate these plants from *S. exigua*. Further study is needed.

9. *Salix geyeriana* Andersson, Sv. Vet.-akad. Öfvers. 15:122. 1858

S. geyeriana var. *argentea* (Bebb) C. K. Schneider; *S. geyeriana* var. *meleina* J. K. Henry

High Cascade Ranges, Southern Sierra Nevada Foothills, High Sierra Nevada, San Bernardino Mts. (disjunct at Big Bear Lake), Modoc Plateau (Dorris, Siskyou Co., Fletcher Cr., Modoc Co., and Warner Mts.), and East of Sierra Nevada (White Mts.). Map 7. British Columbia and Montana southward to California and New Mexico.

Salix geyeriana is similar to, but distinct from, *S. lemmonii*. The two are often difficult to distinguish except on the basis of several variable characters including branch glaucousness, leaf size, leaf blade hair density and color, size and shape of catkins, anther length, petiole length, and chromosome number (Argus 1993). Important differences are chromosome numbers: *S. geyeriana* $2n = 38$, *S. lemmonii* $2n = 76$ (Dorn 1975); and catkin size and shape: *S. geyeriana* catkins are short and subspheric and those of *S. lemmonii* are longer and cylindrical. Hybridization between *S. geyeriana* and *S. lemmonii* is rare but seems to occur in Sierra and Lassen cos. Sympatric populations of these species occur in Modoc Co., Fletcher Cr., Devil's Garden; Mono Co., 23 mi. west of Bridgeport; Plumas Co., Portola and Sierra Valley; Tulare Co., Taylor Meadows, Pine Flat, and Left Stringer; and Nevada Co., Hirshdale, Boca Dam, and Sagehen Creek Field Station. Field studies of these populations may indicate the extent to which the two hybridize and how they can best be separated. See *S. lemmonii*.

Salix geyeriana can be distinguished from *S. drummondiana* by having the abaxial surface of leaf blade moderately silky vs. densely silky, midrib silky vs. midrib glabrous, and margins flat vs. revolute.

10. *Salix gooddingii* C. R. Ball, Bot. Gaz. 11:376. 1905

S. gooddingii var. *variabilis* C. R. Ball; *S. nigra* auct. non Marshall; *S. nigra* Marshall var. *vallicola* Dudley; *S. vallicola* (Dudley) Britton & Shafer

Inner North Coast Ranges (Clear L., Lake Co., and Rumsey, Yolo Co.), Sierra Nevada Foothills, Great Central Valley, South Coast Ranges, Peninsular Ranges, East of Sierra Nevada (White Mts.), Mojave Desert, Sonoran Desert. Map 8. California to Utah and Texas southward to the northern half of Mexico.

Salix gooddingii differs from *S. nigra* by its yellow- to gray-brown branches and the frequent occurrence of pilose ovaries and capsules. The frequency of plants (studied in CAS) with pilose to glabrous ovaries is 54:14; in plants with mature capsules the frequency is about 1:1, indicating that pilosity is lost as fruits mature.

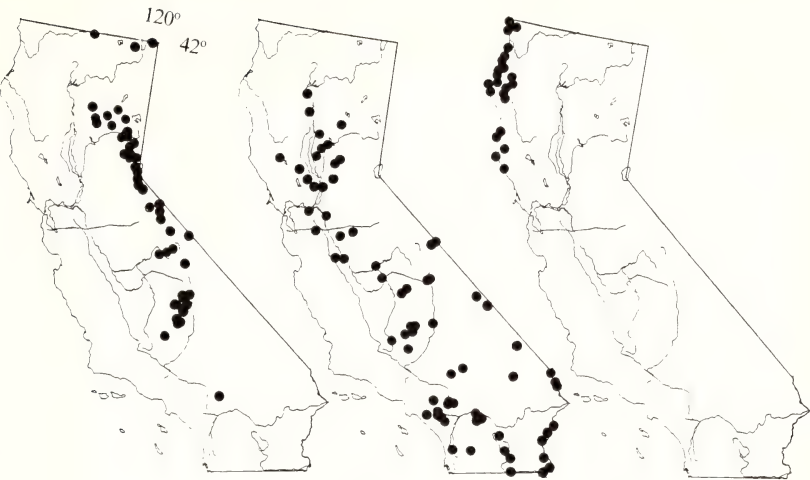


Fig. 7. *Salix geyeriana* Fig. 8. *Salix gooddingii* Fig. 9. *Salix hookeriana*

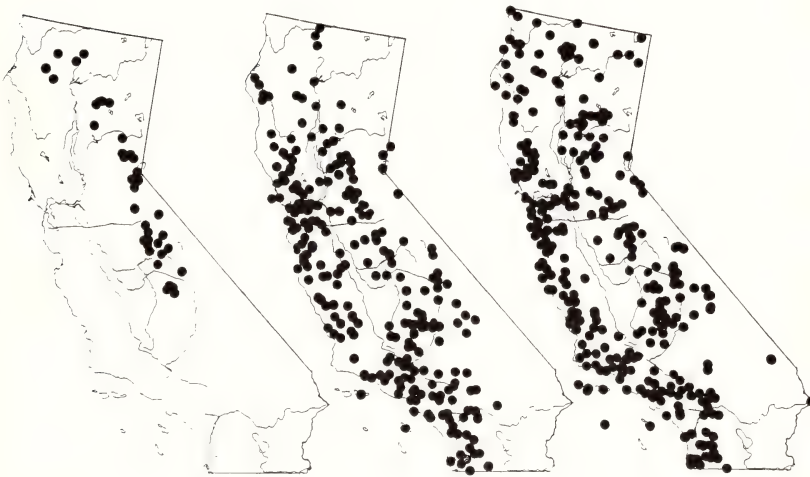


Fig. 10. *Salix jepsonii* Fig. 11. *Salix laevigata* Fig. 12. *Salix lasiolepis*
var. *lasiolepis*

The eastern American *S. nigra* typically has glabrous ovaries, but a specimen collected near Ottawa, Ontario, Canada (*Argus* 13582, CAN) had pilose ovaries indicating that both taxa have the genetic capability of producing pilose ovaries. A search for this character in hundreds of other specimens of *S. nigra* was unsuccessful. The two taxa are distinct, even where they overlap in central Texas, and should be maintained as species.

Occasionally, specimens of *S. gooddingii* may flower a second time in the year by producing catkins in the axil of leaves (*Wilder* 4829, Prado Dam, Riverside Co., 30 Oct. 1970, POM); this character is diagnostic of *S. bonplandiana* Kunth. The possibility that, in *S. gooddingii*, it reflects hybridization with *S. bonplandiana* should be studied (see *S. laevigata*).

11. *Salix hookeriana* Barratt ex Hook. Fl. bor.-amer. 2:145. 1838

S. piperi Bebb

North Coast, Klamath Ranges, Outer North Coast Range. Map 9. Coastal Alaska southward to California.

Salix hookeriana is morphologically variable. Branchlets and leaves are densely villous to glabrous (with indumentum consisting of white hairs or a mixture of white and ferruginous hairs), ovaries are villous to glabrous, and catkins are sessile (flowering precociously [appearing before the leaves]) or on flowering branchlets up to 23 mm long (then flowering coetaneously [appearing with the leaves]). The species is typically densely hairy but glabrous extremes have been named *S. piperi*. This variant occurs with the typical species in northwestern California (mouth of Caspar R, Mendocino Co., and gravel bars of Smith R, Del Norte Co.) and adjacent Oregon. Populations containing intermediates occur at Paine's Cr., Tehama Co., and on gravel floodplains of the Van Duzen R., Humboldt Co. Glabrous plants suggest *S. hookeriana* \times *S. lasiolepis* and among the type material of *S. piperi* is a specimen originally so named. Only the glabrous variant, however, seems to occur in two, high elevation populations (South Yager Cr. and Snow Camp, Humboldt Co., 300–1380 m). Field study of these populations may shed some light on its origin.

Populations in Alaska, which are not sympatric with *S. scouleriana* (a species with leaf indumentum containing ferruginous hairs), have leaf indumentum consisting of only white hairs. From British Columbia south to California indumentum often is a mixture of white and ferruginous hairs. This character may have been introduced into *S. hookeriana* by hybridization and introgression with *S. scouleriana*. These species usually occupy different habitats, the former coastal dunes, marshes, and river floodplains, the latter upland forests. Also, *S. hookeriana* usually lacks stipules and has villous

or tomentose branchlets and petioles; *S. scouleriana* is stipulate and has velutinous branchlets and petioles. Many plants recombine these characters in ways that suggest hybridization and introgression.

12. *Salix jepsonii* C. K. Schneider, J. Arnold Arbor. 1:89. 1919

S. sitchensis Sanson ex Bong. var. *angustifolia* Bebb.; *S. sitchensis* var. *ralphiana* (Jeps.) Jeps.

Klamath Ranges, High Cascade Ranges, High Sierra Nevada. Map 10. Endemic to California and Nevada.

It is difficult to consistently separate *S. jepsonii* from *S. sitchensis*. The only character that seems useful is leaf width; *S. jepsonii* generally has narrower leaves (length/width (2.5) 3.3–7.3) than *S. sitchensis* (length/width 1.7–3.9). Schneider (1919) separated them on stamen number (*S. sitchensis* with one stamen per flower and *S. jepsonii* with two) and, on these grounds, even placed them into different sections. A study of 22 staminate specimens of *S. jepsonii* revealed 17 with two stamens and seven with one. Stamen number was also found to sometimes vary even within a single catkin. *S. jepsonii* generally occurs at higher elevations than *S. sitchensis* and their ranges are largely allopatric. Specimens of *S. jepsonii* from high elevations in Siskyou and Trinity cos. are particularly difficult to separate from *S. sitchensis*. A specimen from Stirling, Butte Co. (A. A. Heller 10832 MO), identified as *S. jepsonii*, strongly resembles *S. sitchensis* but is “out-of-range” for that species. Similarly the holotype of *S. sitchensis* f. *ralphiana* Jepson (Jepson 690 JEPS), tentatively annotated as *S. jepsonii* by both Schneider (in 1919) and Argus (in 1989), resembles *S. sitchensis* but is also “out-of-range”. Crovello (1968) maintained *S. jepsonii* as a distinct “taxospecies” but commented that further study was needed. The hypothesis that *S. jepsonii* originated through hybridization between *S. sitchensis* and *S. drummondiana* needs testing.

13. *Salix laevigata* Bebb, Amer. Naturalist 8:202. 1874

S. bonplandiana Kunth var. *laevigata* (Bebb) Dorn; *S. laevigata* var. *angustifolia* Bebb; *S. laevigata* var. *araquipa* (Jeps.) C. R. Ball; *S. laevigata* var. *congesta* Bebb

Throughout California except for the Modoc Plateau and Sonoran Desert. Gaps occur in the northeastern Klamath Ranges, much of the northern High Sierra Nevada, the eastern Mojave Desert, and the Desert Mts. Map 11. Oregon and Utah southward to California and Arizona.

Salix laevigata is closely related to *S. bonplandiana*. They are separated by leaf shape (length/width: *S. laevigata* 3.3–(4.9)–5.8 vs *S. bonplandiana* 4.4–(6.5)–11.7), stipule length (*S. laevigata* 1.2–(5.2)–12 mm vs. *S. bonplandiana* 0–(1.8)–3.6 mm), and in length

of flowering branchlets on which the pistillate catkins are borne (*S. laevigata* 3–(11.4)–20 mm vs. *S. bonplandiana* 2.5–(6.4)–11 mm). In addition, *S. laevigata* is spring-flowering and has catkins borne on distinct flowering branchlets on branches of the previous year. The catkins of *S. bonplandiana* appear throughout the year and are borne sessile, or on short flowering branchlets, in the axils of long-persistent leaves. The two overlap in northern Baja California where intergradation is suspected. The species in this region need study.

Putative hybrids with *S. gooddingii* have been seen from Kern Co., east of Mt. Mesa, *Dunn, Conrad & Kenney* 20855 (NY); Shasta Co., between Middle Creek Sta. and Keswick, *Heller* 7950 (CAS); and Tehama Co., Red Bluff, *Ball, Smith & Bracelin* 650 (POM).

14. *Salix lasiolepis* Benth. Pl. Hartw. 335. 1857 var. *lasiolepis*

S. lasiolepis var. *bracelinae* C. R. Ball; *S. lasiolepis* var. *falax* Bebb; *S. lutea* var. *nivaria* Jeps.; *S. lasiolepis* var. *sandbergii* (Rydb.) C. R. Ball; *S. tracyi* C. R. Ball

Throughout California. Absent from much of the Mojave and Sonoran Deserts (the record plotted at Parker Dam is in Arizona). Map 12. Washington and Idaho southward to California and Texas and northern and central Mexico.

Several varieties of *S. lasiolepis* have been named (including var. *bigelovii*, var. *sandbergii*, and var. *bracelinae*); but, with the exception of var. *bigelovii* (see below), the separating characters appear to be developmental. Tagged plants from Los Angeles and Siskiyou cos. (UC/JEPS) show such wide variation in leaf shape and in leaf apex shape that early season collections were named var. *bigelovii* and later season collections var. *lasiolepis*. Hybridization also may also contribute to this variation. The highly variable populations in northern coastal regions (Gasquet, Del Norte Co., and Mad R. and Petrolia, Humboldt Co.) suggest hybridization with *S. hookeriana*. The hybrid *S. lasiolepis* × *S. sitchensis* was reported from the San Bruno Mts, San Mateo Co. (McClintock and Knight 1968). This hybrid was not confirmed by this study.

15. *Salix lasiolepis* Benth. var. *bigelovii* (Torr.) Bebb in S. Watson, Bot. Calif. 2:86. 1879

S. bigelovii Torr., Pacif. Rail. Rep. 4:139. 1857

North Coast, Klamath Ranges, Outer and Interior North Coast Ranges, Central Coast, Outer South Coast Ranges, South Coast, Channel Islands. Map 13. Endemic to California and Oregon.

The coastal taxon, *S. lasiolepis* var. *bigelovii*, is a possible ecotype; it differs from var. *lasiolepis* in leaves narrowly to broadly obovate, densely woolly-tomentose on abaxial surface, if becoming

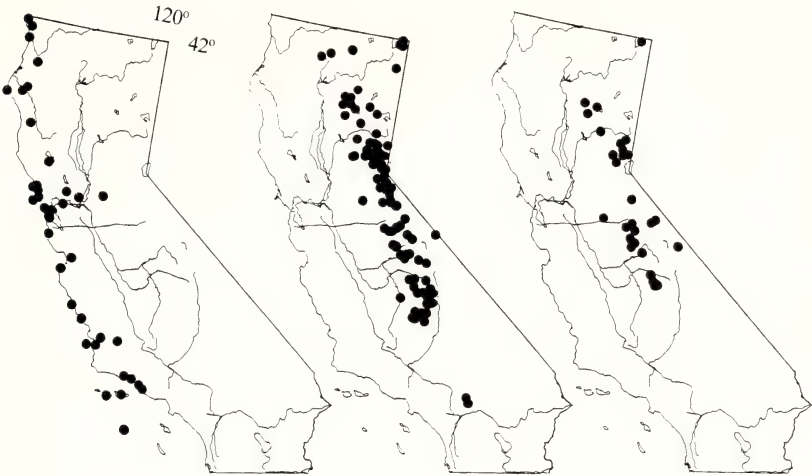


Fig. 13.
● *Salix lasiolepis*
var. *bigelovii*

Fig. 14.
● *Salix lemmonii*

Fig. 15.
● *Salix ligulifolia*

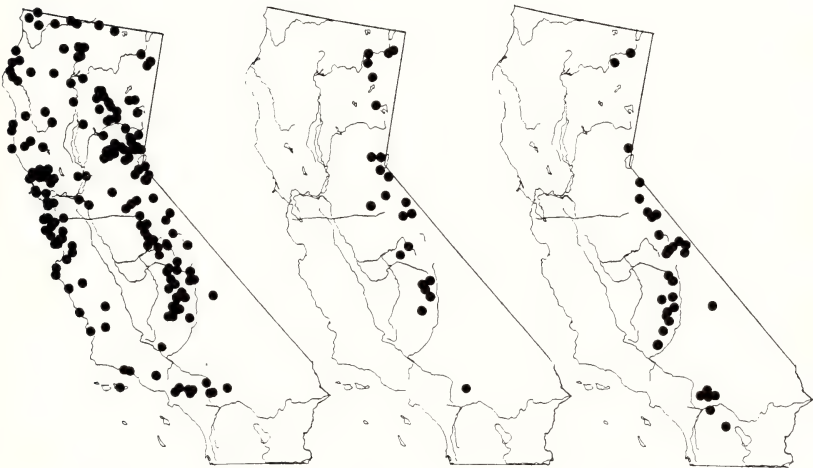


Fig. 16.
● *Salix lucida*
subsp. *lasiandra*

Fig. 17.
● *Salix lucida*
subsp. *caudata*

Fig. 18.
● *Salix lutea*

Maps 13–18.

glabrous, then the blade coarsely veined, and leaf apex generally obtuse to rounded.

16. *Salix lemmonii* Bebb in S. Watson, Bot. Calif. 2:88. 1879

S. austinae Bebb; *S. lemmonii* var. *macrostachya* Bebb; *S. lemmonii* var. *melanopsis* Bebb; *S. lemmonii* var. *sphaerostachya* Bebb

Klamath Ranges (Mt. Eddy), High Cascade Range, High Sierra Nevada, San Bernardino Mts. (disjunct), Modoc Plateau (Goose L., Warner Mts.), East of Sierra Nevada (White Mts.). Map 14. British Columbia and Montana southward to California and Colorado.

A population of *S. lemmonii* on the shore of Webber Lake, Sierra Co. (W. Dudley 5407–5411, 5415, and 5418 (DS)) seems to be intermediate to *S. geyeriana*. The catkins are short for *S. lemmonii* but the floral bracts are dark, the styles distinct, and the leaves are not as densely sericeous as in *S. geyeriana*.

Salix lemmonii exhibits both glaucous and non-glaucous branches and branchlets. Such plants, with a bluish-white bloom, are conspicuous and sometimes thought to be a different taxon. With the exception of Modoc Co., where only the glaucous-stemmed variant seems to occur, both types occur throughout the range of the species. This glaucescence variation is similar to that which occurs in *S. irrorata* Anderson (Argus 1995). It does not seem to be of taxonomic significance.

17. *Salix ligulifolia* (C. R. Ball) C. R. Ball in E. C. Smith, Amer. Midl. Nat. 27:236. 1942

S. eriocephala Michx. var. *ligulifolia* (C. R. Ball) Dorn

High Cascade Range, High Sierra Nevada, Modoc Plateau (Warner Mts.), East of Sierra Nevada (Mono L.). Map 15. Montana and South Dakota southward to California and New Mexico.

See *Salix prolixa*.

18. *Salix lucida* Muhl. subsp. *lasiandra* (Benth.) E. Murray, Kalmia 15:11. 1984 “1985”

S. lasiandra Benth. Pl. Hartweg. 335. 1857; *S. lasiandra* var. *abramsii* C. R. Ball; *S. lasiandra* var. *lancifolia* (Anderson) Bebb

Throughout California except San Joaquin Valley, Peninsular Ranges, most of Mojave Desert (known only at Darwin Springs), and Sonoran Desert. Map 16. Alaska and western Northwest Territories southward to California and New Mexico.

See *Salix lucida* subsp. *caudata*.

19. *Salix lucida* Muhl. subsp. *caudata* (Nutt.) E. Murray, Kalmia 15:11. 1984 “1985”

S. caudata (Nutt.) A. A. Heller; *S. lasiandra* var. *bryantiana* C.

R. Ball & Bracelin; *S. lasiandra* var. *caudata* (Nutt.) Sudw.; *S. lasiandra* var. *fendleriana* (Anderson) Bebb; *S. pentandra* L. [var.] *caudata* Nutt., North Am. Sylva 1:61. 1842

High Sierra Nevada, San Bernardino Mts. (disjunct), Modoc Plateau (Goose L. and Pit River, Modoc Co.), East of Sierra Nevada (Bridgeport and Tioga L., Mono Co.). Map 17. Alaska and western Northwest Territories southward to California, Colorado, and South Dakota.

Salix lucida subsp. *caudata* is separated from subsp. *lasiandra* by having leaves nonglaucous abaxially and with stomata on both adaxial and abaxial surfaces (amphistomatous) (Argus 1986a). Numerous specimens of subsp. *lasiandra* (plants with leaves glaucous abaxially) are also amphistomatous. Such intermediates (CAS and DS) occur in Fresno Co., Kings Canyon; Inyo Co., Whitney Portal; Modoc Co., Alturas; Mono Co., Convict L. and Bridgeport; Nevada Co., lower end of Donner L., Boca, and Truckee; Plumas Co., Portola and Butterfly Cr.; Shasta Co., La Maine; Tulare Co., various localities; and Tuolumne Co., Twain Harte. Sympatric populations in Big Bear Valley and Big Bear Lake, San Bernardino Co., could be studied to determine if these taxa deserve even subspecies rank.

20. *Salix lutea* Nutt. N. Amer. Sylva 1:63. 1842

S. cordata Muhl. var. *watsonii* Bebb; *S. lutea* var. *watsonii* (Bebb) Jeps.; *S. eriocephala* Michx. var. *watsonii* (Bebb) Dorn; *S. rigida* Muhl. var. *watsonii* (Bebb) Cronquist

Central and southern High Sierra Nevada, Southwestern California (disjunct in San Bernardino and San Jacinto mts.), Modoc Plateau (Alturas and Adin), East of Sierra Nevada, Mojave Desert (disjunct in Paramint Mts.). Map 18. Northwest Territories eastward to Quebec and southward to California, Arizona and Iowa.

Salix lutea differs from the related *S. eriocephala* in having one-year-old branches yellowish and smooth, lacking an exfoliating epidermis, and branchlets glabrous or, if hairy, not with long, soft, wavy hairs. It has been treated as a variety of *S. eriocephala* by Dorn (1995), but its phenetic distance from other members of *S. sect. Cordatae* supports species rank (Argus 1997).

21. *Salix melanopsis* Nutt. N. Amer. Sylva 1:78. 1842

S. exigua Nutt. var. *gracilipes* (C. R. Ball) Cronquist; *S. melanopsis* var. *bolanderiana* (Rowlee) C. K. Schneider; *S. exigua* subsp. *melanopsis* (Nutt.) Cronquist

North Coast (Gasquet and Smith R., Del Norte Co.), Klamath Ranges (Seiad Valley, Siskiyou Co.), Cascade Range Foothills (Chico, Butte Co.), High Cascade Range (Chester, Plumas Co.), northern



Fig. 19.
 ● *Salix melanopsis*
 ○ *Salix nivalis*



Fig. 20.
 ● *Salix orestera*



Fig. 21.
 ● *Salix petrophila*
 ○ *Salix sessilifolia*



Fig. 22.
 ● *Salix planifolia*
 ○ *Salix prolixa*



Fig. 23.
 ● *Salix scouleriana*



Fig. 24.
 ● *Salix sitchensis*

Maps 19–24.

Sierra Nevada Foothills (Spenceville and confluence of Bear R. and Wolf Cr., Nevada Co.), southern Sierra Nevada Foothills (Kernville, Kern Co.), High Sierra Nevada, Sacramento Valley (Knights Ferry, Stanislaus Co.), Modoc Plateau (Parker Cr., Modoc Co.). Map 19. British Columbia and Alberta southward to California and Wyoming.

22. *Salix nivalis* Hook. Fl. bor-amer. 2:152. 1838

S. nivalis var. *saximontana* (Rydb.) C. K. Schneider; *S. reticulata* L. subsp. *nivalis* (Hook.) A. Löve, D. Löve & B. M. Kapoor

Central High Sierra Nevada. Map 19. British Columbia and Alberta southward in the Cordillera to California and Colorado.

Salix nivalis is treated here as a species because hybridization in the region of overlap was localized and indistinct (Argus 1986b) and the phenetic distance between *S. nivalis* and *S. reticulata* (Argus 1997) supports specific rank.

23. *Salix orestera* C. K. Schneider, J. Arnold. Arbor. 1:164. 1920

S. commutata Bebb var. *rubicunda* Jeps.; *S. glauca* L. var. *orestera* (C. K. Schneider) Jeps.

Southern Sierra Nevada Foothills, High Sierra Nevada, East of Sierra Nevada (White Mts.). Map 20. Oregon, California, and Nevada.

Salix orestera is sometimes difficult to separate from *S. lemmonii* and *S. eastwoodiae*. The possibility that it originated through hybridization between the latter two species could be studied in the Kaiser Pass area, Fresno Co. (CAS), where all three species occur.

24. *Salix petrophila* Rydb. Bull. N. Y. Bot. Gard. 1:268. 1899

S. arctica Pall. var. *antiplasta* sensu auct.; *S. arctica* Pall. var. *petraea* (Andersson) Bebb; *S. arctica* Pall. subsp. *petraea* (Andersson) A. Löve, D. Löve & B. M. Kapoor

High Cascade Range (Mt. Lassen), High Sierra Nevada. Map. 21. Oregon and Montana southward in the Cordillera to California and New Mexico.

In modern floras *Salix petrophila* is treated as a synonym of *S. arctica* (e.g., Argus 1993, Goodrich 1983; Dorn 1977), sometimes as *S. arctica* var. *petraea* (Hitchcock et al. 1964). A study of specimens in NA and NY and a phenetic study (Argus 1997) suggest that it is a distinct species. It differs from *S. arctica* in leaves lacking long, straight hairs on the abaxial surface, especially the proximal leaves; floral bracts brown to tawny, not dark brown to black, bracts usually glabrous or clothed with wavy hairs, not the long straight hairs characteristic of *S. arctica*; and branchlets glabrous.

In California, *S. petrophila* resembles *S. cascadiensis* Cockerell in its narrow, sharply pointed leaves and pale-colored floral bracts. Specimens originally identified as *S. cascadiensis* (Alexander & Kellogg 3376 and Hoover 4483 NA) proved to be *S. petrophila*. The phenetic distance between *S. petrophila* and *S. cascadiensis* is very close (Argus 1997); these taxa cluster with *S. arctica* and *S. spenophylla* Skvortsov and are placed with them in *S. sect. Diplodictya* C. K. Schneider (syn. *S. sect. Arcticae* Rydb). These species deserve further study.

25. *Salix planifolia* Pursh, Fl. Am. Sept. 2:611. 1814 subsp. *planifolia*

S. monica Bebb; *Salix phylicifolia* L. var. *monica* (Bebb) Jeps.; *S. phylicifolia* var. *planifolia* (Pursh) Cronquist; *S. planifolia* var. *monica* (Bebb) C. K. Schneider

High Sierra Nevada. Map 22. Alaska to Newfoundland, southward in the east in the mountains of New England and in the west to California, New Mexico, and South Dakota.

In California, *S. planifolia* is represented by a subalpine variant, (sometimes called var. *monica*). These plants are prostrate to erect shrubs (up to 1 m), with diminutive (20–43 mm long), elliptic, usually amphistomatous leaves, and small catkins (10–45 mm long). It was not recognized as a distinct taxon in *The Jepson Manual* (Argus 1993) but it deserves further study.

26. *Salix prolixa* Andersson, Monogr. Salicum 94. 1867

S. cordata sensu auct.; *S. cordata* Muhl. var. *mackenzieana* Hook.; *S. eriocephala* Michx. var. *mackenzieana* (Hook.) Dorn; *S. mackenzieana* (Hook.) Andersson; *S. rigida* Muhl. var. *mackenzieana* (Hook.) Cronquist

Klamath Range (Yreka, Siskiyou Co.), High Cascade Range (Glazier, Siskiyou Co.), northern High Sierra Nevada (Greenville, Quincy, and Meadow Valley Cr., Plumas Co; Camassia Bend, CA Hwy 89, Sierra Co.), Modoc Plateau (Alturas and Contrall's Mill, Modoc Co.). Map 22. The Yukon and Northwest territories southward to California and Wyoming.

In their overall morphology, *S. prolixa* and *S. ligulifolia* are very similar. They may be separated by *S. prolixa* having narrowly elliptic to obovate leaves (L/W 2.4–4.5), base often cordate, stipules with an obtuse to rounded apex, and usually longer stipes (1.3–4.2 mm long); *S. ligulifolia* has ligulate to very narrowly elliptic leaves (L/W 2.9–6.4), base rarely cordate, stipules with acute to acuminate apex, and usually shorter stipes (0.9–2.5 mm long).

This species has been treated as a variety of *S. eriocephala* by

Dorn (1995), but its phenetic distance from other members of *S. sect. Cordatae* supports species rank (Argus 1996).

S. reticulata L. subsp. *nivalis* = *S. nivalis*.

27. *Salix scouleriana* Barratt ex Hook. Fl. Bor.-amer. 2:145. 1838

S. scouleriana var. *coetanea* C. R. Ball; *S. scouleriana* var. *flavescens* (Nutt.) J. K. Henry; *S. scouleriana* f. *poikila* (C. K. Schneider) C. K. Schneider

North Coast, Klamath Ranges, Outer and High North Coast Ranges, High Cascade Range, southern Sierra Nevada Foothills (Upper Lucas Cr., Tehachapi-Kernville region, Kern Co.), High Sierra Nevada, Central Coast, San Francisco Bay Area, San Bernardino Mts. (disjunct), Modoc Plateau (including Warner Mts.). Map 23. Alaska and the western Northwest Territories eastward to Saskatchewan and southward to California, New Mexico, South Dakota, and northern Mexico.

Salix scouleriana occurs on the Smith R., Del Norte Co., along with *S. hookeriana* and *S. lasiolepis*. Its flowers are unusual in having hairy ovaries, long, broad-lobed stigmas, and longer anthers, but vegetatively it compares with specimens of *S. scouleriana* that lack velutinous petioles and branchlets. All three species may have leaves with ferruginous hairs. In *S. scouleriana* these hairs differ in having a prominently reddish base which makes the leaf surface appear punctate.

28. *Salix sessilifolia* Nutt. N. Amer. Sylva 1:68. 1842

S. parksiana C. R. Ball

North Coast, Klamath Ranges, Outer North Coast Range. Map 21. Coastal British Columbia to California.

Salix parksiana may be the hybrid *S. melanopsis* × *S. sessilifolia*.

29. *Salix sitchensis* Sanson ex Bong. Mem. Acad. St. Petersburg. 6. 2: 162. 1832 [1833?]

S. coulteri Andersson; *S. sitchensis* var. *coulteri* (Andersson) Jeps.; *S. sitchensis* var. *parviflora* (Jeps.) Jeps.

North Coast, Klamath Ranges, Outer and Inner North Coast Ranges, Central Coast, San Francisco Bay Area, and South Coast (Santa Barbara). Map 24. Alaska southward to California and Montana.

Plants with leaves densely lanate to sericeous-lanate abaxially have been named *S. coulteri*. This variant does not seem to occur outside of northern California, but in California it is sympatric with typical *S. sitchensis*, which usually has leaves densely sericeous abaxially. Crovello (1968) correctly treated them as conspecific.

Similar extreme variation in leaf indumentum also occur in *S. scouleriana*. The genetics of these variants has not been studied.

TAXONOMY OF INTRODUCED AND NATURALIZED WILLOWS

Few specimens of introduced *Salix* were seen from California. Only the tree willows, *S. alba*, *S. babylonica*, their cultivars and hybrids, and the shrubby *S. purpurea* L. seem to be represented in herbaria. Their naturalized status is uncertain.

1. *Salix alba* L. var. *vitellina* (L.) Stokes, Bot. Mat. Med. 4:506. 1812

S. alba var. *tristis* (Ser.) Gaudin; *S. vitellina* L., Sp. Pl. 1016. 1753; *S. alba* subsp. *vitellina* (L.) Shübler & Martens

Salix × *ehrhartiana* G. Meyer, Chloris han. 486. 1836

S. alba × *S. pentandra*

Salix × *rubens* Schrank, Baier. fl. 1:226. 1789

S. alba × *S. fragilis*

Salix × *sepulcralis* Simonk. Oesterr. Bot. Zeitschr. 40:424. 1890

S. alba var. *vitellina* × *S. babylonica*

Specimens representing typical *S. alba* were not seen; all specimens were referred to var. *vitellina* or the above hybrids.

2. *Salix babylonica* L. Sp. Pl. 2:1017. 1753

Salix × *pendulina* Wenderoth, Schrift. Nat. Ges. Marb. 2:235. 1831 [pro sp.]

S. babylonica × *S. fragilis*

Salix × *pendulina* cv *blanda*

S. × *blanda* Andersson, Monogr. Salicum 50. 1867

Specimens resembling *S. babylonica* or possibly *S.* × *pendulina* cv. *blanda*, were seen from Santa Barbara and Santa Clara cos. Other specimens were the hybrid *S.* × *sepulcralis* (see *S. alba*). *Salix* × *pendulina* is represented by three cultivars one of which is cv. *blanda*.

KEY TO THE COMMONLY CULTIVATED TREE WILLOWS (see also Meikle 1984).

1. Twigs erect or spreading 2
2. Twigs brown or olive 3
3. Leaf blade dull or silky adaxially, hair white 4
4. Leaf blade persistently silky adaxially *S. alba* var. *alba*
- 4'. Leaf blade becoming glabrous adaxially *S.* × *rubens*

| | |
|---|---|
| 3'. Leaf blade glossy adaxially, hair white and rusty | <i>S. ×ehrhartiana</i> |
| 2'. Twigs yellow or golden | <i>S. alba</i> var. <i>vitellina</i> |
| 1'. Twigs pendent | 5 |
| 5. Twigs yellow or golden; leaf blade silky or glabrate | <i>S. alba</i> var. <i>vitellina</i> cv. <i>pendula</i> |
| 5'. Twigs brown or olive; leaf blade glabrate | 6 |
| 6. Catkin on distinct, leafy shoots, generally greater than 2 cm | <i>S. ×sepulcralis</i> |
| 6'. Catkin subsessile | |
| 7. Catkins generally less than 2 cm, ovary abruptly tapering to style | <i>S. babylonica</i> |
| 7'. Catkins generally more than 2 cm, ovary gradually tapering to style | <i>S. ×pendulina</i> |

PHYTOGEOGRAPHY

Salix occur throughout California. The geographic region with the greatest *Salix* diversity (Table 1) is the Sierra Nevada Region (21 taxa), followed by Northwestern California (18 taxa), Cascade Ranges (14 taxa), Modoc Plateau (13 taxa), East of Sierra Nevada (12 taxa), Southwestern California (11 taxa), Central Western California (9 taxa), Great Central Valley (7 taxa), Mojave Desert (5 taxa), and the Sonoran Desert (3 taxa). The subregion with the greatest *Salix* diversity is the High Sierra Nevada Subregion (20 taxa) followed closely by the Klamath Ranges (16 taxa) and the High Cascade Ranges (14 taxa). *Salix exigua* and *S. lasiolepis* occur in all subregions; *S. laevigata* is missing only from the Sonoran Desert Subregion; and *S. lucida* subsp. *lasiandra* is missing only in the Sonoran Desert Subregion and the Peninsular Ranges Subregion (San Jacinto Mts.). The species with the smallest range in California is *S. brachycarpa*, known only from the Central High Sierra Nevada (Major & Bamberg 1963). Wide disjunctions occur within the mountains of Southern California: *S. geyeriana*, *S. lemmonii*, *S. lucida* subsp. *caudata*, *S. lutea*, and *S. scouleriana* all occur as disjuncts in the San Bernardino Mts., and *S. eastwoodiae* is disjunct in the San Jacinto Mts.

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TABLE 1. GEOGRAPHICAL OCCURRENCE OF *SALIX* IN CALIFORNIA. NW = Northwestern California Region, CaR = Cascade Ranges Region, SN = Sierra Nevada Region, GV = Great Central Valley Region, CW = Central Western California Region, SW = Southwestern California Region, MP = Modoc Plateau Region, SNE = East of Sierra Nevada Region, DMOj = Mojave Desert Region, DSon = Sonoran Desert Region (following Hickman 1993).

| Taxa | NW | CaR | SN | GV | CW | SW | MP | SNE | DMoj | DSon |
|---------------------------------|----|-----|----|----|----|----|----|-----|------|------|
| <i>S. hebbiana</i> | | | | | | | X | | | |
| <i>S. boothii</i> | X | X | X | | | | X | X | | |
| <i>S. breweri</i> | X | | | | X | | | | | |
| <i>S. brachycarpa</i> | | | X | | | | | | | |
| <i>S. delnortensis</i> | X | | | | | | | | | |
| <i>S. drummondiana</i> | | | X | | | | | | | |
| <i>S. eastwoodiae</i> | X | X | | X | | | X | X | | |
| <i>S. exigua</i> | X | X | X | X | X | X | X | X | X | X |
| <i>S. geyeriana</i> | | X | X | | | X | X | X | | |
| <i>S. gooddingii</i> | X | | X | | X | X | | X | X | X |
| <i>S. hookeriana</i> | X | | | | | | | | | |
| <i>S. jepsonii</i> | X | X | X | | | | | | | |
| <i>S. laevigata</i> | X | X | X | X | X | X | | X | X | |
| <i>S. lasiolepis bigelovii</i> | X | | | | X | | | | | |
| <i>S. lasiolepis lasiolepis</i> | X | X | X | X | X | X | X | X | X | X |
| <i>S. lemmonii</i> | X | X | X | | | X | X | X | | |
| <i>S. ligulifolia</i> | | X | X | | | X | X | X | | |
| <i>S. lucida caudata</i> | | X | X | | | X | X | X | | |
| <i>S. lucida lasiandra</i> | X | X | X | X | X | X | X | X | X | |
| <i>S. lutea</i> | | | X | | | X | | | | |
| <i>S. melanopsis</i> | X | X | X | X | | | X | | | |
| <i>S. nivalis</i> | | | X | | | | | | | |
| <i>S. orestera</i> | | | X | | | | | X | | |
| <i>S. petrophila</i> | | X | X | | | | | | | |
| <i>S. planifolia</i> | | | X | | | | | | | |
| <i>S. proluxa</i> | | X | X | | X | | | | | |
| <i>S. scouleriana</i> | X | X | X | | | X | X | | | |
| <i>S. sessilifolia</i> | X | X | | | | | | | | |
| <i>S. sitchensis</i> | X | | | | X | X | | | | |

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ARCTOSTAPHYLOS INCOGNITA, A NEW SPECIES AND ITS PHENETIC RELATIONSHIP TO OTHER MANZANITAS OF BAJA CALIFORNIA

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ABSTRACT

Arctostaphylos incognita Keeley, Massihi, Delgadillo & Hiraes is a new diploid, burl-forming manzanita endemic to rhyolitic soils in the northern coast range of Baja California. The intensely glaucous and glabrous foliage, coupled with highly reduced bracts on nascent panicles, bears remarkable resemblance to that of another Baja California manzanita, *A. peninsularis*, which is restricted to granitic soils in the interior ranges of the Sierra San Pedro Mártir and Sierra Juárez. The extreme differences in fruit structure, however, readily distinguish these two species. Unlike the round fruits with leathery pericarp and solid endocarp stones of *A. peninsularis*, the new *A. incognita* has depressed fruits with mealy pericarp and separable nutlets, indistinguishable from those of *A. glandulosa*. Principal components analysis based on 57 phenetic characters showed that the widespread *A. glandulosa* and *A. glauca* were clearly separable from the five species endemic to Baja California; *A. incognita*, *A. peninsularis*, *A. australis*, *A. bolensis*, and *A. moranii*. Principal components analysis on the endemic species alone showed that *A. incognita* was closest to *A. peninsularis* and further analysis showed that *A. australis* and *A. moranii* overlapped a great deal in their morphology. Also we report here chromosome numbers for *A. incognita* (n=13), for the first time for *A. australis* (n=13), and *A. moranii* (n=26).

RESUMEN

Arctostaphylos incognita Keeley, Massihi, Delgadillo & Hiraes, es una nueva especie de manzanita diploide que forma nudos y es endémica de las cordilleras costeras del norte de Baja California. Su follaje intensamente glauco y glabro, con brácteas reducidas en panículas nacientes, tienen una notable semejanza a *A. peninsularis*, una especie restringida a las cordilleras interiores de Sierra Juárez y Sierra San Pedro Mártir. La estructura del fruto en *A. incognita* es muy diferente a las de *A. peninsularis*, en cambio frutos depresos y aplanados con pericarpo granuloso y nuecesillas separables son indistinguibles en *A. glandulosa*. Un análisis de componentes principales basado en 57 caracteres fenéticos, mostró claramente una separación de mayormente endémicas a Baja California; *A. incognita*, *A. peninsularis*, *A. australis*, *A. bolensis* y *A. moranii*. Por otra parte, el análisis de componentes principales de sólo las especies endémicas mostraron que *A. incognita* esta proxima a *A. pen-*

insularis, y *A. australis* y *A. moranii* al traslaparse una gran parte de sus características morfológicas. También, se reporta el número cromosómico de *A. incognita* (n=13), *A. australis* (n=13), y *A. moranii* (n=26).

The manzanita flora of northern Baja California comprises nine shrub species, four of which are endemic to the state; three are restricted to the coast ranges and one to the interior ranges. The coast ranges species include *Arctostaphylos australis* Eastwood, a non-burl-forming species distributed in widely disjunct populations, mostly south of Ensenada (latitude 31°50'). *Arctostaphylos bolensis* Wells is another non-burl-forming species, which was described recently from a single population at about 600 m elevation on the north side of Cerro Bolo, 25 km south of Tecate (Wells 1992). Although apparently not widespread, it also occurs at about the same elevation on Cerro Italia, approximately 10 km south of the type locality (*J. E. Keeley 2337* RSA). Another localized endemic is the burl-forming *A. moranii* Wells, which is restricted to north of Ensenada, between Cerro Ensenada and El Tigre.

In the interior ranges, *A. peninsularis* Wells is the only manzanita endemic to Baja California; early reports of this species in coastal San Diego County were in error and represent *A. rainbowensis* Keeley & Massihi and interior San Diego County reports of this species (Keeley and Massihi 1994) are based on specimens that require further study. In the northern part of *A. peninsularis*'s range, in the Sierra Juárez, it is a non-burl-forming single-stemmed arborescent shrub (*A. peninsularis* ssp. *juarezensis* Keeley, Massihi, & Goar 1992, Keeley and Massihi 1994). Farther south, largely in the Sierra San Pedro Mártir, it is a low-growing, multi-stemmed resprouting shrub. Although the other Baja manzanitas are very widespread outside of Mexico, within Baja California they too are restricted to either the coast or the interior ranges. *Arctostaphylos glandulosa* Eastw. with one of the widest ranges in the genus, is a burl-forming shrub restricted to the coast ranges, extending inland only to the foothills east of Ensenada. The non-burl-forming *A. pungens* Kunth, *A. pringlei* Parry, and *A. patula* Greene are restricted to high elevations in the interior ranges, and are widespread in southwestern North America. The only species not restricted to coastal or interior ranges is the widespread non-burl-forming *A. glauca* Lindl., occurring on the interior sides of the coast ranges and well into the interior ranges.

Recent collections have uncovered a new manzanita species endemic to the coast range north of Ensenada, Baja California. This taxon is described here and a multivariate phenetic comparison is made between it and associated *Arctostaphylos*.

SPECIES TREATMENT

Arctostaphylos incognita J. Keeley, A. Massihi, J. Delgadillo, & S. Hirales. sp. nov. (Fig. 1)—TYPE: MEXICO, Baja California,

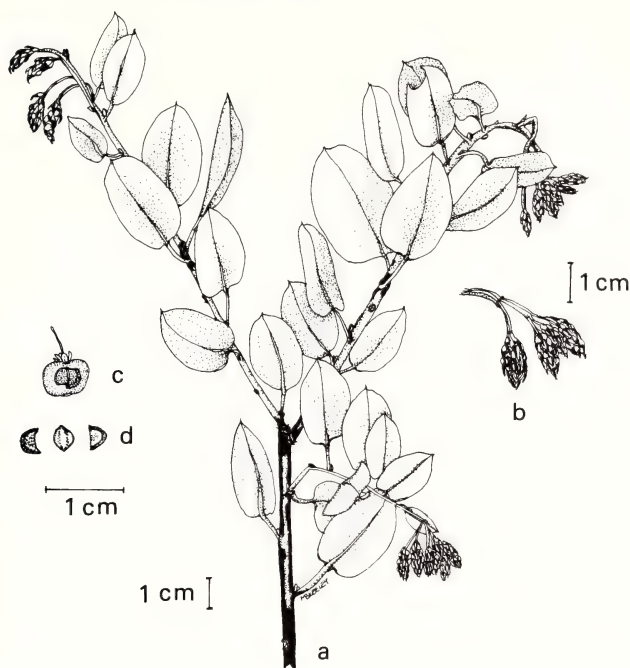


FIG. 1. *Arctostaphylos incognita* (J. Keeley 24108). a. Branchlet with nascent inflorescences. b. Nascent inflorescence. c. Whole fruit. d. Pyrenes. By Melanie Baer Keeley.

NE slope of Cerro Italia, W of Carmen Serdán, elevation 620 m, 9 August 1993, *J. E. Keeley 24108* (holotype, RSA; isotypes, BCUGX, CAS, SD, MO).

Frutices erecti aut arbores, 1–4 m alti; caudex tumescens, repululans post combustum; cortex laevis rufus; ramuli glabris; laminae isofaciales, numero stomatarum adaxiales et abaxiales aequalis, ellipticae, glaucae, apices rotundi, basis acuti-rotundi, petioli 4–6 mm longi; inflorescentiae nascens descendens, paniculate, ramuli 5–6, glabrati; bracteae 1–2 mm longae, subulatae, acuminatae, glabrae; pedicelli 5–7 mm longi, glabri; corolla urceolatae, 5–6 mm longae, 4–5 mm latae, albae; ovaria glabra; drupae depressae, 5–6 mm longae, 8–9 mm latae, glabrae, rubrae, mesocarpia crassa, separabiles.

Erect shrub or arborescent, 1–4 m high, with large globose burl on unburned shrub or platform-like on resprouted shrubs. Bark red-brown, smooth. Branchlets glabrous and glaucous. Leaves isofacial with equal number of stomata on adaxial and abaxial sides, blades 35–40 mm long, 25–30 mm wide, elliptic, glabrous, and heavily glaucous, base acute to rounded with rounded apex, petioles 4–6 mm. Panicle with 5–6 branches; bracts 1–2 mm, overlapping, del-

toid-subulate, keeled, upper-half early marcescent; rachis glabrous. Corolla urceolate, 5-lobed, white, pubescent inside, 5–6 mm long, 4–5 mm wide; inflated filaments bases densely hairy; ovary glabrous; pedicel glabrous; sepals reflexed. Fruit depressed, 5–6 mm long, 8–9 mm wide, glabrous, red; mesocarp thick and mealy, nutlets separable. Flowering January–February. $n=13$ (J. Keeley & A. Massihi). The epithet was inspired by the fact that, although populations of this species are easily visible from one of the two major highways in northern Baja California, it has long been overlooked by botanists. The arborescent stature and glaucous foliage of *A. incognita* provide a perfect disguise as it resembles *A. glauca*, which is common near the highway.

Distribution. In addition to the type locality on the NE side of Cerro Italia and surrounding hills, we have made additional collection of this species approximately 15 km SW, along a dirt road W of San Jose de la Zorra. All of these collections were from rhyolite soils between 300 and 700 m. North of the type locality, at about 600 m on basaltic soil on the N side of Cerro Bolo there are populations of manzanitas very similar to *A. incognita*, however, as one ascends to the peak this taxon intergrades morphologically with *A. glandulosa*. Wells (1987) describes the intensely glaucous population at the top of Cerro Bolo Peak (1200 m) as *A. glandulosa* ssp. *adamsii* forma *wieriana* Wells.

Paratypes. MEXICO, Baja California, 24.5 km NE of La Misión on road to San Jose de la Zorra, 340 m, 30 August 1993, *J. Keeley 24210* (RSA); 22 km NE of La Misión on road to San Jose de la Zorra, 30 August 1993, 370 m, *J. Keeley 24256* (RSA); SE of Ejido Carmen Serdán, 530 m, 27 July 1993, *Massihi, Hiraes, & J. Keeley 23520* (RSA); 2 km SE of Carmen Serdán, 550 m, 19 February 1994, *J. Keeley 25237* (RSA).

PHENETIC ANALYSIS OF *A. INCOGNITA* AND OTHER BAJA CALIFORNIA MANZANITAS

Phenetic data were collected from herbarium specimens and used to compare *A. incognita* with other species from Baja California. Extensive collections of this new species and other Baja California manzanitas were made during late summer, when both fruits and nascent inflorescences were available (specimens are housed at RSA and BCUGX).

METHODS

Species. The phenetic analysis included the Baja California species most similar to *A. incognita* (sample sizes and collection locations are in Table 1). Sample sizes were in part a function of

TABLE 1. SPECIES, SAMPLE SIZES AND LOCATION OF *ARCTOSTAPHYLOS* USED IN THE PHENETIC ANALYSIS. Letter codes used in Figures 2-4 are included.

| Species | (Code) | Specimens sampled | Collecting locations |
|--|--------|-------------------|---|
| <i>A. australis</i> | (A) | 25 | South of Ensenada |
| <i>A. bolensis</i> | (B) | 26 | Type locality, North side of Cerro Bolo |
| <i>A. incognita</i> | (I) | 70 | Throughout its range (see text) |
| <i>A. glandulosa</i> | (g) | 30 | Southern San Diego County |
| <i>A. glandulosa</i> var. <i>adamsii</i> | (C) | 22 | Cerro Bolo Peak |
| forma <i>wieriana</i> | (G) | 30 | Southern San Diego County |
| <i>A. glauca</i> | | | North Baja California |
| <i>A. moranii</i> | (M) | 22 | Type locality, near San Jose de las Minas |
| <i>A. peninsularis</i> | (P) | 80 | Sierra Juárez & Sierra San Pedro Mártir |

TABLE 2. CHARACTERS USED IN PRINCIPLE COMPONENTS ANALYSIS AND FACTOR LOADINGS FOR FIGURES 2, 3, AND 4. Characters lacking scores were dropped due to zero variance.

| Character | Figure 2 | | Figure 3 | | Figure 4 | |
|---------------------------------|----------|----------|----------|----------|----------|----------|
| | Factor 1 | Factor 2 | Factor 1 | Factor 2 | Factor 1 | Factor 2 |
| Presence or absence of burl | 0.46 | -0.38 | -0.19 | -0.68 | -0.06 | 0.82 |
| Leaf blade length | 0.24 | -0.22 | 0.12 | -0.67 | 0.01 | -0.26 |
| Leaf blade width | -0.05 | -0.11 | 0.14 | -0.50 | -0.16 | -0.32 |
| Ratio leaf length/width | 0.21 | 0.01 | -0.42 | -0.19 | 0.12 | -0.76 |
| Basal angle | 0.38 | -0.32 | -0.01 | -0.31 | 0.14 | 0.35 |
| Apical angle | 0.39 | -0.10 | -0.05 | -0.24 | 0.07 | 0.13 |
| Blade shape | 0.26 | -0.08 | -0.10 | -0.04 | -0.11 | -0.11 |
| Petiole length | -0.17 | -0.10 | 0.24 | -0.24 | 0.43 | -0.25 |
| Leaf color | 0.09 | -0.03 | 0.11 | -0.16 | -0.03 | -0.06 |
| Leaf glaucousness | 0.63 | -0.08 | 0.55 | -0.36 | 0.24 | 0.21 |
| Leaf scabrousness | 0.91 | 0.26 | 0.36 | 0.08 | 0.17 | -0.06 |
| Density of abaxial stomata | 0.50 | 0.46 | -0.07 | -0.34 | -0.84 | 0.04 |
| Density of adaxial stomata | -0.01 | 0.47 | 0.02 | -0.27 | -0.85 | -0.07 |
| Abaxial stomata/adaxial stomata | 0.68 | 0.15 | -0.14 | -0.09 | 0.20 | 0.26 |
| Branchlet pubescence | 0.89 | 0.13 | 0.87 | 0.25 | 0.56 | 0.11 |
| Petiole pubescence | 0.90 | 0.14 | 0.86 | 0.24 | 0.44 | 0.29 |
| New leaf blade pubescence | 0.84 | 0.17 | 0.81 | 0.15 | -0.26 | 0.35 |
| Old leaf blade pubescence | 0.64 | 0.10 | 0.66 | 0.10 | -0.63 | 0.47 |
| Rachis pubescence | 0.88 | 0.10 | 0.78 | 0.16 | 0.77 | -0.07 |
| Pedicel pubescence | 0.73 | 0.59 | 0.68 | 0.26 | 0.46 | 0.22 |
| Fruit pubescence | 0.51 | 0.19 | — | — | — | — |
| Branchlet glandularity | 0.90 | 0.21 | 0.42 | 0.22 | 0.67 | -0.20 |
| Petiole glandularity | 0.71 | 0.17 | 0.24 | 0.14 | 0.36 | -0.09 |
| New leaf blade glandularity | 0.81 | 0.25 | 0.07 | -0.02 | -0.16 | -0.07 |
| Old leaf blade glandularity | 0.51 | 0.12 | -0.02 | -0.07 | — | — |
| Rachis glandularity | 0.87 | 0.22 | 0.50 | 0.27 | 0.86 | -0.37 |
| Pedicel glandularity | 0.48 | 0.79 | 0.48 | 0.21 | 0.45 | 0.11 |
| Fruit glandularity | -0.06 | 0.89 | -0.07 | 0.13 | — | — |
| Inflorescence length | -0.18 | -0.02 | 0.16 | 0.09 | -0.04 | 0.31 |
| Number of rachis branches | -0.09 | -0.33 | 0.40 | -0.16 | -0.17 | 0.13 |
| Nascent orientation | 0.07 | -0.14 | 0.64 | 0.04 | -0.88 | 0.21 |
| Bract spacing | -0.56 | 0.38 | 0.31 | 0.02 | -0.81 | 0.07 |
| Bract keel | -0.66 | -0.03 | -0.61 | -0.44 | 0.14 | 0.32 |
| Bract shape | -0.77 | -0.19 | -0.05 | -0.16 | -0.74 | -0.10 |
| Bract marcescence | -0.34 | -0.64 | -0.23 | 0.70 | -0.14 | 0.03 |
| Bract reflexed | -0.24 | 0.76 | 0.31 | 0.05 | -0.10 | -0.24 |
| Bract length | | | | | | |
| (subtending inflorescence) | 0.79 | 0.35 | 0.20 | 0.53 | 0.87 | -0.30 |
| (subtending flower buds) | 0.67 | 0.47 | 0.43 | 0.07 | 0.71 | 0.23 |
| Pedicel length | -0.16 | -0.02 | -0.20 | 0.26 | 0.58 | -0.13 |
| Sepal shape | -0.41 | -0.61 | 0.48 | -0.53 | 0.22 | -0.29 |
| Sepal reflexed | 0.48 | -0.36 | 0.09 | -0.11 | 0.43 | -0.36 |
| Fruit color | -0.39 | 0.26 | -0.02 | -0.25 | 0.29 | -0.11 |
| Fruit length | -0.52 | 0.76 | -0.30 | 0.79 | 0.03 | 0.70 |
| Fruit width | -0.14 | 0.74 | -0.67 | 0.09 | 0.13 | 0.68 |
| Fruit width/fruit length | 0.58 | -0.19 | -0.26 | -0.77 | 0.16 | -0.03 |
| Fruit weight | -0.41 | 0.84 | -0.70 | 0.44 | 0.38 | 0.78 |
| Pericarp weight | -0.26 | 0.68 | -0.63 | 0.02 | 0.29 | 0.48 |
| Endocarp weight | -0.44 | 0.83 | -0.59 | 0.59 | 0.32 | 0.74 |

TABLE 2. CONTINUED

| Character | Figure 2 | | Figure 3 | | Figure 4 | |
|------------------------------|----------|----------|----------|----------|----------|----------|
| | Factor 1 | Factor 2 | Factor 1 | Factor 2 | Factor 1 | Factor 2 |
| Fruit weight/endocarp weight | -0.40 | 0.28 | 0.18 | 0.49 | -0.04 | 0.06 |
| Mesocarp texture | -0.12 | 0.06 | 0.06 | 0.09 | -0.01 | 0.16 |
| Endocarp segments | 0.44 | -0.33 | -0.23 | -0.79 | 0.09 | 0.09 |
| Endocarp lateral ridges | 0.51 | -0.29 | -0.82 | -0.16 | 0.08 | 0.28 |
| Endocarp sculpturing | 0.34 | -0.17 | -0.87 | 0.02 | -0.10 | 0.08 |
| Endocarp apiculate | -0.71 | 0.33 | -0.46 | 0.70 | 0.58 | -0.21 |
| Stone height | -0.56 | 0.74 | -0.43 | 0.83 | 0.33 | 0.65 |
| Stone width | -0.34 | 0.83 | -0.53 | 0.67 | 0.48 | 0.60 |
| Stone width/stone height | 0.65 | 0.03 | -0.10 | -0.48 | 0.17 | -0.10 |

availability of complete specimens, which included both nascent inflorescences and mature fruits. Three Baja California species, *A. pungens*, *A. pringlei*, and *A. patula* were not included in our comparison because they differ markedly from the other manzanitas, both morphologically and ecologically, and do not occur within the range of *A. incognita*.

Analysis. We used 57 characters in this study; 16 continuous quantitative, 2 meristic, 33 qualitative, and 6 calculated ratios (Table 2). Qualitative characters were given a ranking on a scale from 1 to 5. For quantitative characters, two samples were measured or weighted for each specimen and the mean was used in the analysis. As in previous studies (Keeley and Massihi 1994), patterns of variation suggested that more sampling of the same specimen was of less value than sampling more individuals in the population. In other words, despite the differences in sample size, the within specimen variance was seldom greater than the between specimen variance. Additionally, for most reproductive characters, a sample size of 2 was all that was available on each herbarium sheet. All character states were standardized by transforming each variable with a z-score calculated by subtracting each observation from the mean of all individuals, and dividing by the standard deviation. This matrix was used for ordination with principal components analysis using SYSTAT for Windows, Version 5.05 (Evanston, IL).

Stomatal distribution was determined from epidermal peels (2×2 cm) made with clear polish and examined at $25\times$. The mean of five different sections of a peel were recorded for each specimen. Chromosome counts were made from buds collected in February for one population of *A. incognita* (*J. Keeley* 25237 RSA) and for a single population of two other Baja California manzanitas lacking published counts: *A. australis* (*J. Keeley* 25239 RSA) and *A. moranii* (*J. Keeley* 25238 RSA). Developing anthers were squashed in

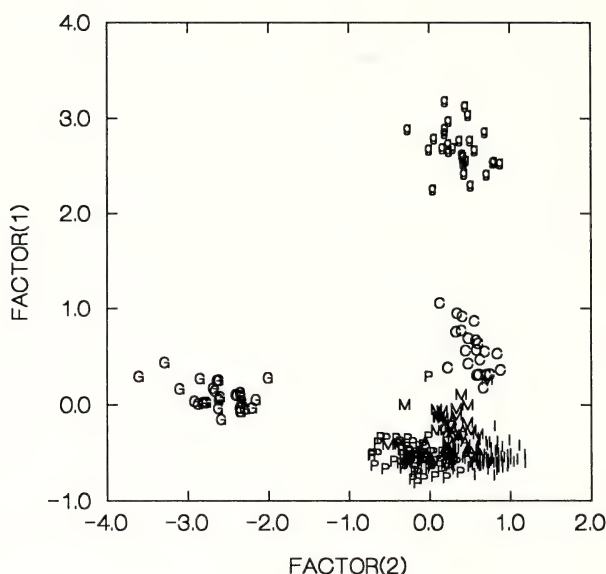


FIG. 2. Principal components analysis with all species listed in Table 1. Species are designated by letter codes listed in Table 1. Factor loading scores are in Table 2.

acetocarmine and viewed at $100\times$. This character was not used in the principal components analysis because *A. peninsularis* and *A. bolensis* have not been counted.

RESULTS

The first two components or factors of the principal components analysis for 261 specimens, including *A. incognita*, and the six other Baja California species distributed within its range, are shown in Figure 2. *Arctostaphylos incognita* and the other four Baja California endemic species are clearly differentiated from the widespread *A. glandulosa* on the factor 1 axis and from the widespread *A. glauca* on the factor 2 axis. The first factor explained 29% of the variance and the second factor explained 17% of the variance.

The factor loadings indicate the extent to which each character used in this analysis contributes to the variance in its respective plane and are shown in Table 2. Based on the component loadings for factor 1, it is apparent that the characters most important in distinguishing *A. glandulosa* from the five endemic species (and from *A. glauca*) are leaf and stem indument, and inflorescence bract length and shape. Component loadings for factor 2 indicated that fruit size and bract characters are most responsible for distinguishing *A. glauca* from the endemics (and from *A. glandulosa*). In this analysis, the Cerro Bolo Peak population of *A. glandulosa* (Wells 1987

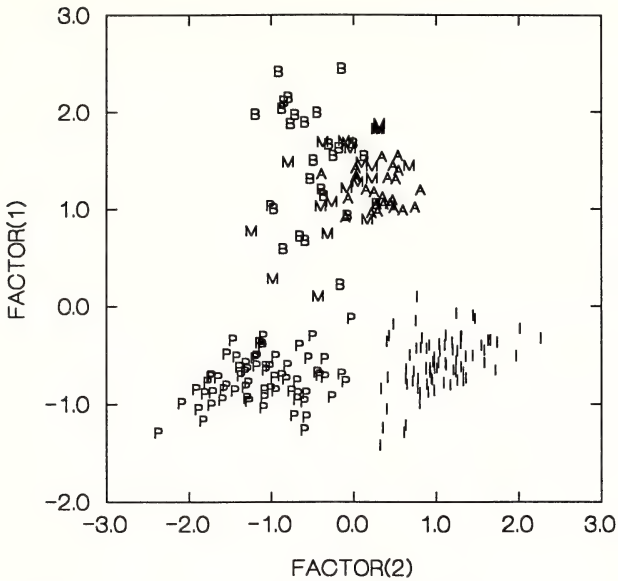


FIG. 3. Principal components analysis with *Arctostaphylos incognita* (I), *A. peninsularis* (P), *A. australis* (A), *A. bolensis* (B), and *A. moranii* (M). Factor loading scores are in Table 2.

refers these plants to ssp. *adamsii* forma *wieriana* Wells), is morphologically more similar to the Baja endemic species than to San Diego County *A. glandulosa* (Fig. 2). Although the Cerro Bolo *A. glandulosa* overlap with *A. bolensis*, which is also from Cerro Bolo, it is well separated from *A. incognita* (Fig. 2).

Principal components analysis for the five endemic species alone showed *A. incognita* and *A. peninsularis* can be distinguished readily from *A. australis*, *A. bolensis*, and *A. moranii* (Fig. 3). The first factor explained 20% of the variance and was the primary axis along which *A. incognita* and *A. peninsularis* separated from the other three endemic species. The component loading scores indicated that indument and a few fruit and leaf characters were most important in separation on the factor 1 axis (Table 2). *Arctostaphylos incognita* separated from *A. peninsularis* along the factor 2 axis and, based on the component loading scores, separation was largely due to fruit characters (Table 2).

Although *A. australis*, *A. bolensis*, and *A. moranii* are not differentiated in either of the above principal components analyses, they can be distinguished when analyzed alone (Fig. 4 and Table 2). *Arctostaphylos bolensis* separated clearly along the factor 1 axis, and this factor explained 19% of the variance. Factor 2 accounted

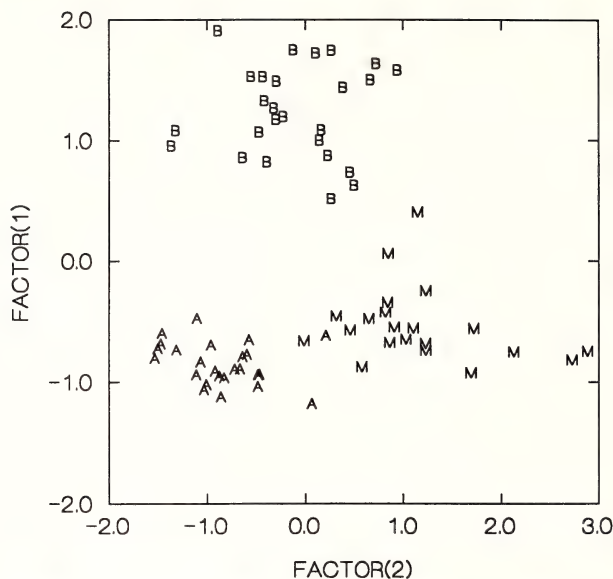


FIG. 4. Principal components analysis with *Arctostaphylos australis* (A), *A. bolensis* (B), and *A. moranii* (M). Factor loading scores are in Table 2.

for only 10% of the variance and still left some overlap between *A. australis* and *A. moranii*.

Chromosome counts were made on several individuals of *A. incognita* from one population ($n=13$), and for a single individual of *A. australis* ($n=13$) and *A. moranii* ($n=26$).

DISCUSSION

Based on the patterns of morphological similarity (Figs. 2 and 3), we hypothesize that *A. incognita* is related to *A. peninsularis*. Indeed, in the absence of reproductive structures, these species are remarkably similar and not readily distinguished. They have a similar leaf shape and similar foliage indument; leaves and branchlets are intensely glaucous and glabrous (Table 3). The only measurable differences in vegetative characteristics are larger leaves with a more acute base in *A. incognita*. Even the presence of nascent inflorescences would not assist in separating these two taxa as both have panicles with highly reduced bracts, although *A. incognita* panicles are more highly branched than those of *A. peninsularis*. However, fruit characteristics are radically different between these species (Table 3). The flattened or depressed fruits with mealy endocarp and separable nutlets of *A. incognita* contrasts sharply with the larger round fruits, leathery to papery pericarp, and solid stone of fused nutlets of *A. peninsularis*. The fact that these taxa differ in the struc-

ture of the exocarp, mesocarp, and endocarp, differences that nearly span the range of variation in the genus, supports their recognition as separate species.

A comparison of fruit characteristics (Table 3) reveals that *Arctostaphylos incognita* shares nearly identical fruit characteristics with *A. glandulosa*, suggesting the hypothesis that this species also has played a role in the ancestry of *A. incognita*. Tests of this hypothesis should include *A. glandulosa* ssp. *adamsii* forma *wieriana* from Cerro Bolo Peak, as it closely resembles *A. incognita* in its intensely glaucous leaves and reduced nascent inflorescence bracts.

Of course a phenetic analysis such as this can not unequivocally rule out convergence in accounting for the similarity of these taxa, but hybridization should be given serious consideration. There are countless cases of apparent hybridization in the genus and, although all are suggested by patterns of phenetic variation, a few have been supported with genetic evidence (Ellstrand et al. 1987; Nason et al. 1992). Based on the vegetative similarity between *A. incognita* and *A. peninsularis*, and the fruit similarity between *A. incognita* and *A. glandulosa*, it is tempting to hypothesize that the origin of this newly described species may involve an ancient hybridization between these two well known species.

Other scenarios, however, are possible, particularly since such parentage can not explain all characteristics associated with this new species. For example, Ball et al. (1983; see also Ellstrand et al. 1987 for genetic confirmation) showed that tolerance to water stress in *Arctostaphylos* hybrids was intermediate between a lower elevation species and a higher elevation species. *Arctostaphylos incognita* occupies a more arid habitat than either *A. peninsularis* or *A. glandulosa*. *Arctostaphylos peninsularis* is restricted to the interior ranges, above 1000 m on granitic soils (with one rare occurrence on an unusual slate outcrop in the Sierra San Pedro Mártir (*J. Keeley* 23181–23191 LOC). In contrast, *A. incognita* is restricted to much lower elevations on rhyolitic soils in the interior side of the coast ranges. Although, *A. glandulosa* is widespread on rhyolitic soils, in the interior part of the coast ranges it is distributed at higher elevations than *A. incognita*. The arid habitat occupied by *A. incognita* is shared by *A. glauca* and thus, if we had included physiological and ecological characters in our principal components analysis we may have found a closer relationship between these two species than is evident in Figure 2.

Our comparison of *A. incognita* with the other Baja California *Arctostaphylos* raises a question about distinctness of *A. australis* and *A. moranii* (Fig. 4). Both *A. australis* and *A. moranii* have relatively thin nascent inflorescences that stand erect, with buds relatively widely spaced, characteristics heavily weighted in *Arctostaphylos* taxonomy and found in more northerly distributed species

TABLE 3. COMPARISON OF CHARACTERISTICS OF SELECTED BAJA CALIFORNIA *AKTOSTAPHYLOS*. Mean \pm standard error. Glaucous scale: 1 = intensely glaucous-5 = non-glaucous and lustrous. Bract marcescence scale: 1 = tips never withered-5 = tips always withered. Bract spacing scale: 1 = bracts strongly overlapping-5 = bracts very widely spaced.

| Character | <i>A. incognita</i> | <i>A. peninsularis</i> | <i>A. glandulosa</i> | <i>A. glauca</i> | <i>A. australis</i> | <i>A. moranii</i> | <i>A. bolensis</i> |
|---------------------------------------|---------------------|------------------------|-------------------------------|---------------------|---------------------|-------------------|-------------------------|
| Sample size: | 80 | 70 | 30 | 30 | 25 | 22 | 26 |
| Chromosome #: | $n = 13$ | ? | $n = 26$ | $n = 13$ | $n = 13$ | $n = 26$ | ? |
| Burl: | Yes | Yes & no | Yes (no)* | No | No | Yes | No |
| Leaves | | | | | | | |
| Length (mm): | 39.5 ± 0.6 | 29.0 ± 0.5 | 37.3 ± 1.0 | 33.5 ± 1.2 | 35.2 ± 1.3 | 32.8 ± 1.3 | 34.3 ± 0.8 |
| Ratio length/width: | 1.6 ± 0.0 | 1.6 ± 0.0 | 1.8 ± 0.1 | 1.4 ± 0.0 | 1.5 ± 0.1 | 1.6 ± 0.1 | 1.6 ± 0.0 |
| Basal angle (°): | 27.7 ± 1.1 | 19.6 ± 1.3 | 31.4 ± 1.7 | 9.7 ± 1.5 | 18.7 ± 2.3 | 25.1 ± 2.4 | 19.7 ± 2.9 |
| Glaucous (1-5 scale): | 2.0 ± 0.0 | 1.1 ± 0.0 | 3.3 ± 0.1 | 1.5 ± 0.1 | 2.2 ± 0.1 | 2.4 ± 0.1 | 2.5 ± 0.1 |
| Scabrous: | No | No | Yes | No | No | No | No |
| Stomata | | | | | | | |
| Abaxial density (#/mm ²): | 24.2 ± 0.3 | 22.2 ± 0.8 | 40.6 ± 1.6 | 31.5 ± 1.2 | 29.3 ± 0.7 | 22.4 ± 0.5 | 16.1 ± 0.3 |
| Ratio (ab-/adaxial): | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.6 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 |
| Branchlet indument: | Glabrous & glaucous | Glabrous & glaucous | Pubescent to glandular-hispid | Glabrous & glaucous | Glabrous | Pubescent | Glandular-hispid |
| Inflorescences | | | | | | | |
| Nascent orientation: | Descending | Descending | Descending (erect)** | Descending | Erect | Erect | Descending to ascending |
| Branches (#): | 6.0 ± 0.1 | 2.2 ± 0.1 | 2.0 ± 0.2 | 2.1 ± 0.2 | 4.0 ± 0.3 | 4.6 ± 0.3 | 3.4 ± 0.3 |
| Basal bract lengths (mm): | 0.1 ± 0.1 | 1.9 ± 0.3 | 12.4 ± 0.4 | 2.2 ± 0.5 | 0.0 ± 0.0 | 0.7 ± 0.4 | 5.3 ± 0.3 |
| Bract marcescence (1-5 scale): | 4.9 ± 0.1 | 2.8 ± 0.1 | 1.0 ± 0.0 | 1.8 ± 0.2 | 3.0 ± 0.2 | 3.0 ± 0.2 | 2.6 ± 0.2 |
| Bract spacing (1-5 scale): | 1.9 ± 0.1 | 2.0 ± 0.0 | 1.0 ± 0.0 | 3.9 ± 0.1 | 3.6 ± 0.2 | 2.5 ± 0.2 | 1.5 ± 0.1 |

TABLE 3. CONTINUED

| Character | <i>A. incognita</i> | <i>A. peninsularis</i> | <i>A. glandulosa</i> | <i>A. glauca</i> | <i>A. australis</i> | <i>A. moranii</i> | <i>A. bolensis</i> |
|---------------------|---------------------|------------------------|----------------------|------------------|---------------------|-------------------|--------------------|
| Fruits | | | | | | | |
| Ratio width/height: | 1.5 ± 0.0 | 1.0 ± 0.0 | 1.7 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.0 ± 0.0 |
| Mass (mg): | 198.6 ± 7.9 | 292.0 ± 10.5 | 184.5 ± 10.4 | 924.0 ± 38.7 | 81.9 ± 6.9 | 197.6 ± 19.0 | 142.7 ± 11.1 |
| Endocarp segments: | 3.6 ± 0.1 | 1.0 ± 0.0 | 3.4 ± 0.1 | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.1 ± 0.1 | 1.1 ± 0.1 |
| Coloration: | Red | Orange-red | Orange-red | Brown | Tan-red | Red | Red |
| Mesocarp: | Mealy | Papery | Mealy | Papery | Leathery | Leathery | Leathery |

* Although a vigorous burl-forming resprouter throughout its entire range, a single non-burl-forming, non-sprouting population of *A. glandulosa* is known from south of Ensenada (*J. Keeley 24150-24163* RSA).

** Several *A. glandulosa* populations in Baja California have erect nascent inflorescences (*J. Keeley 17860-17931* RSA).

such as *A. stanfordiana* Parry. This similarity between *A. australis* and *A. moranii* likely contributed to Knight (1984) originally describing this latter taxon as *A. australis* var. *sericea* Knight, a name apparently ignored by Wells (1992) in naming *A. moranii*. If chromosome number had been included in our principal components analysis, the tetraploid *Arctostaphylos moranii* likely would have separated more distinctly from the diploid *A. australis* (cf. Fig. 4). In light of the ease with which *Arctostaphylos* hybridize (and arguments presented by Schierenbeck et al. 1992), it seems likely that *A. moranii* represents an allopolyploid. We hypothesize that its origin involves a cross between *A. australis* and the tetraploid, burl-forming *A. glandulosa*; the latter species possesses all of the characteristics that distinguish *A. moranii* from *A. australis*; a burl, foliage pubescence and leaf coloration differences. Indeed, in the chaparral E of El Tigre, there are populations with intermediate characteristics and recombinations between *A. glandulosa* and *A. moranii* (J. Keeley 17087–17203 RSA)

CONCLUSIONS

In light of the apparent ease of hybridization and introgression in *Arctostaphylos*, it may prove difficult to test any hypothesis on the origin of *A. incognita*. It seems evident that the apparently high incidence of hybridization in the genus has led to a reticulate pattern of variation, and this is supported by the pattern of species recombining different combinations of traits as seen in Table 3.

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ECOLOGY OF *ARCTOMECON CALIFORNICA* AND *A. MERRIAMII* (PAPAVERACEAE) IN THE MOJAVE DESERT

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ABSTRACT

Arctomecon (Papaveraceae) is composed of three rare gypsophilous species in the northeastern Mojave Desert. In order to effectively manage the remaining populations of these rare plants, which are increasingly being impacted by anthropogenic disturbance, the life history attributes, reproductive biology, vegetative associates and edaphic requirements were investigated for two species in southern Nevada: *Arctomecon californica* and *A. merriamii*. Loss of reproductive potential was highest for both species at the bud and capsule stages, and highest post-reproductive mortality occurred during the seedling stage. *Arctomecon californica* was reproductively self-incompatible, while *A. merriamii* was able to self-pollinate as well as outcross. Both species occurred in vegetation types that were quantitatively distinct and therefore unique relative to typical Mojave Desert plant assemblages. *Arctomecon* also occurred on gypsum-derived soils that were different from off-site locations, most notably in sulfur and calcium contents. Hypotheses as to why *Arctomecon* can establish on gypsum soil, and what role this soil requirement plays in the rarity of this taxa, are considered in light of these results. Habitat specificity, especially for *A. californica*, leads to the conclusion that gypsum outcrops must be preserved in order to ensure the survival of *Arctomecon* species in the Mojave Desert.

INTRODUCTION

The Endangered Species Act of 1973 has led to increased attention to species that are potentially threatened with extinction. The scientific literature is beginning to address this issue with population-level studies on rare plants (Menges and Gawler 1986; Fiedler 1987; Freas and Murphy 1988; Mehrhoff 1989). Data collection on life history parameters is necessary in order to manage species properly (Harper 1979; Owen and Rosentreter 1992), which can also serve to answer ecological and evolutionary questions (Meagher et al. 1978). Although the demographics of some species have been investigated, many rare plant species have no available demographic or functional data. Studies have shown that rare plants are often restricted to certain habitats (Menges 1990) or to a specific soil type (Nelson and Harper 1991); this endemism can contribute to extreme population fluctuations, which can lead to extinction of local populations or entire species (Kruckeberg and Rabinowitz 1985).

One such group of plants is the genus *Arctomecon* (Papavera-

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ceae), which consists of three rare perennial species that inhabit gypsum soils in the Mojave Desert (Meyer 1986). *Arctomecon californica* Torr. and Frem., the golden bear-claw poppy, is found in northern Arizona and southern Nevada on gypsiferous soils. It is listed by the state of Nevada as Critically Endangered, and by the Federal Government as a Category 2 candidate species (Morefield and Knight 1992). *Arctomecon merriamii* Cov., the white bear-claw poppy, occurs in both California and Nevada (Janish 1977), and is also listed by the Federal Government as a Category 2 candidate species (Morefield and Knight 1992). A third species, *A. humilis*, the dwarf bear-claw poppy, is located only in Washington County, Utah, and is federally listed as an Endangered Species. Its gypsum habitat is in danger of destruction by the growth of the city of St. George as well as off-road vehicle use (Nelson and Harper 1991).

Research on the population ecology of *A. humilis* has been conducted (Nelson and Harper 1991), but comparable studies for the other two species of *Arctomecon* have not been published. The goals of this research were to obtain an understanding of the life history and reproductive ecology of *A. californica* and *A. merriamii* in their native habitats, and to describe the vegetation and soils for sites that contain populations of each species. The interaction of these components undoubtedly play an important role in the success of *Arctomecon* species in their respective habitats. As a result, this information is critically needed in order to successfully manage each species to prevent them from federal listing and thus the threat of becoming extinct in all or part of their geographical range.

METHODS

Study Sites

Studies of the two *Arctomecon* species were conducted at several locations in the Mojave Desert, a region that receives only 10–15 cm of precipitation per year, most of which occurs in the winter months. Temperature extremes range from -5°C to 49°C , so both freezing and heat stresses can be important determinants of the distribution of perennial plants in the region.

Three study sites were selected for *Arctomecon californica* within Lake Mead National Recreation Area: (1) near Overton Beach, Clark County, Nevada ($36^{\circ}25'\text{N}$, $114^{\circ}25'\text{W}$, 433 m elev.), 97 km NE of Las Vegas; (2) near Stewart Point, Clark County, Nevada ($36^{\circ}22'\text{N}$, $114^{\circ}24'\text{W}$, 396 m elev.), 90 km east of Las Vegas; and (3) near Temple Bar, Mohave County, Arizona ($36^{\circ}05'\text{N}$, $114^{\circ}25'\text{W}$, 430 m elev.), 161 km southeast of Las Vegas.

Arctomecon merriamii was studied at Ash Meadows National Wildlife Refuge in Nye County, Nevada ($36^{\circ}25'\text{N}$, $116^{\circ}20'\text{W}$, 610

m elev.), located 161 km northwest of Las Vegas. This area is under the protection of the United States Fish and Wildlife Service.

Population Structure, Life History, and Reproductive Ecology

Arctomecon species are herbaceous perennials that form basal rosettes with deep taproots. In their first year, they grow strictly vegetatively and will flower in the second year if there is adequate rainfall. After initial flowering and seed set, they can live several more years and have multiple flowering events. They also tend to form clonal plants with multiple rosettes as they age.

Individuals in each population were mapped using four 10 m² (1 × 10 m) transects that were placed in a systematic random fashion through the habitat. Plants were not individually mapped except for seedlings, which were marked with colored toothpicks and mapped using individual coordinates within a grid (Lesica 1987). Demographic data on each population were collected monthly from May 1992 to September 1993. The diameter of the basal rosette of each plant in the transects was obtained once every three months, increasing to once every two weeks during the flowering season. During flowering, the number of buds, flowers, and capsules were counted for each marked plant, and a sample of capsules was collected to determine the number of seeds per capsule. Comparisons of flowering parameters between sites and age classes within sites were made using a non-parametric Kruskal-Wallis H-test (SAS statistical software).

Mature plants were tested for the ability to self-pollinate by bagging individual buds with a lightweight, draw-string nylon material to prevent insect pollination. Controls were established as buds on the same plant that were marked with string but were not prevented from cross-pollinating. Both control and experimental buds were collected when mature and measured for viable seed set. Results were compared using t-tests, and are reported for *A. californica* from the Overton Beach study site only.

Vegetation and Soils

Data for vegetation analysis were collected on sites where *Arc-tomecon* was found, and at adjacent off-site areas where no poppies were found. Density, frequency, and cover data for *A. californica* were collected using a minimum of 30 randomly placed 1 m² (1 × 1 m) quadrats. Due to the extremely limited distribution of *A. merriamii*, circular plots ranging in size from 1 to 4 m radius (3–50 m²) were used.

Percent Similarity indices were calculated for on- and off-site locations at each major site using species composition data. Percent Similarity between on- and off-site locations was calculated as

$$\text{Percent Similarity} = 1.0 - 0.5 (\sum p_a - p_b) = \sum \min (p_a \text{ or } p_b)$$

where p_a was the decimal Importance Value (0 to 1) for each given species in sample A (i.e., on-site) and p_b was the decimal importance for the same species in sample B (i.e., off-site) (Whittaker 1975). The Coefficient of Community was also calculated between sites, as determined by

$$\text{Coefficient of Community} = 2S_{ab} / (S_a + S_b)$$

where S_a and S_b were the number of species in samples A and B, respectively, and S_{ab} was the number of species found in both samples (Whittaker 1975).

Soils were collected on each site with a soil corer in a random grid pattern ($N = 7$ for *A. californica*, $N = 5$ for *A. merriamii*). Soils were collected for *A. californica* from on- and off-site locations, as well as from sites that appeared similar in texture and color to the on-site location (i.e., visually appeared to be a similar gypsum outcrop) but where no *Arctomecon* were present. [Gypsum outcrops that contain *Arctomecon* populations tend to have a "badlands" appearance in which the soils are whitish in color, fluffy in texture, and tend to form raised crusts that are easily disturbed; off-site locations tend to be flat, compacted, stony surfaces that are often covered with a cemented desert pavement.] Soil cores were separated in the field into surface 0–5 cm depth and 6–15 cm depth increments, stored in separate sealed soil tins, and were immediately transported back to the laboratory. The same methodology was used for *A. merriamii*, but visually similar soils without *Arctomecon* present were not sampled. Soils were analyzed by A & L Western Agricultural Laboratories (Modesto, CA) for pH, percent organic matter, cation exchange capacity, soluble salts, total phosphorous, potassium, magnesium, calcium, sodium, sulfur, and zinc, and percent base saturation of potassium, magnesium, calcium, hydrogen, and sodium. Major components of the soil were compared between sites with Pearson product-moment correlation coefficients using MSTAT statistical software.

RESULTS

Life History and Reproductive Ecology

Data collected for both *Arctomecon californica* and *A. merriamii* were divided into size classes based on logical divisions of the plant rosette diameter, probable age, and percent flowering per size class (Table 1; ages provided are approximate, particularly the 1- and 2-yr-old plants, whereas seedlings and juveniles were accurately determined).

Overall survivorship of *A. californica* over the length of the study

TABLE 1. SIZE CLASS DESCRIPTIONS FOR *ARCTOMECON CALIFORNICA* POPULATIONS AT THREE STUDY SITES (OVERTON BEACH (OB), STEWART POINT (SP), AND TEMPLE BAR (TB)), AND FOR *A. MERRIAMII* AT ASH MEADOWS (AM).

| Size class | Rosette diameter (cm) | Estimated age | % flowering | | | |
|------------|-----------------------|-----------------|-----------------------|-----|-----|---------------------|
| | | | <i>A. californica</i> | | | <i>A. merriamii</i> |
| | | | OB | SP | TB | AM |
| 1 | 0.0–0.9 | Seedling | 0 | 0 | 0 | 0 |
| 2 | 1.0–4.9 | 1 yr juvenile | 0 | 0 | 0 | 0 |
| 3 | 5.0–7.4 | 1–2 yr juvenile | 0 | 0 | 0 | 0 |
| 4 | 7.5–11.4 | 2–2+ yrs | 73 | 100 | 100 | 83 |
| 5 | 11.5–20.9 | 2–2+ yrs | 100 | 100 | 100 | 100 |
| 6 | 21.0–44.0 | 2+ yrs | 100 | 100 | 100 | 100 |

(May 1992 to July 1993) was very low for all three sites, ranging from a minimum of 14% at Stewarts Point to a high of 38% at Temple Bar (Table 2). *Arctomecon merriamii*, on the other hand, showed over a four-fold increase in the number of plants from May 1992 to May 1993. Populations fluctuated widely for both species (Table 2), with *A. californica* showing a pronounced change in population numbers at the Stewart Point site. However, no such change was observed at the other two sites. There were over 300 *A. californica* recruits in 1993, but most died during the hot, dry summer months of June through August. *Arctomecon merriamii* showed a gradual decline in numbers after peak recruitment in April.

Mortality in each size class indicated that the smallest plants had the highest annual mortality (Fig. 1); seedlings (size class 1) exhibited 60–87% mortality for *A. californica* and 39% for *A. merriamii*. For *A. californica*, mortality in the larger size classes differed between the three sites. Size-specific mortality for *A. californica* was approximately 60% for seedlings at Overton Beach and Temple Bar

TABLE 2. DENSITY (PLANTS M⁻²) OF *ARCTOMECON CALIFORNICA* AT THREE SITES AND *ARCTOMECON MERRIAMII* AT ONE SITE FROM MAY 1992 TO JULY 1993. Site abbreviations are Overton Beach (OB), Stewart Point (SP) and Temple Bar (TB) for *A. californica* and Ash Meadows (AM) for *A. merriamii*.

| Year | Month | <i>A. californica</i> | | | <i>A. merriamii</i> |
|------|----------|-----------------------|------|-----|---------------------|
| | | OB | SP | TB | AM |
| 1992 | May | 8.2 | 12.4 | 7.1 | 1.5 |
| | December | 1.6 | 8.2 | 3.3 | 1.4 |
| 1993 | February | 1.5 | 8.0 | 3.3 | 1.3 |
| | March | 2.2 | 18.2 | 3.8 | 5.8 |
| | April | 2.4 | 31.6 | 4.0 | 7.7 |
| | May | 2.2 | 23.1 | 2.7 | 6.5 |
| | July | 1.5 | 1.8 | 2.7 | 4.4 |

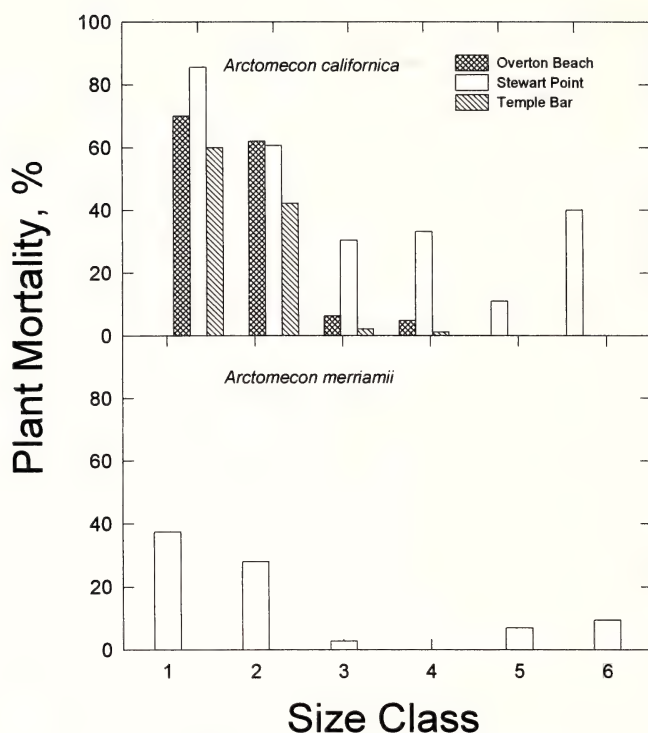


FIG. 1. Percent plant mortality for *Arctomecon californica* (top) and *A. merriamii* (bottom), by size class (see Table 1), from May 1992 to September 1993.

and 80% at Stewart Point. These site differences were also consistent at the larger size classes, as *A. californica* populations at Overton Beach and Temple Bar had very low mortality rates (<5%) in size classes 3 through 6, whereas average mortality of *A. californica* populations at Stewart Point averaged about 25% in these larger size classes (Fig. 1).

Reproductive attrition is defined as the number of buds, flowers and capsules which did not produce seed on each individual plant (i.e., lost reproductive potential). This loss, by size class, showed that *A. californica* lost between 10% and 50% of its reproductive potential across all sites and size classes 3 through 6, and *A. merriamii* exhibited a 2% to 26% reproductive attrition for size classes 4 through 6 (Fig. 2). However, there were no statistically significant differences in reproductive attrition between size classes for *A. californica* ($P = 0.068$) or for *A. merriamii* ($P = 0.234$). In *A. californica*, the Stewart Point populations had the highest reproductive attrition at the largest size classes (35–45% at Stewart Point versus 10–25% at the other two sites).

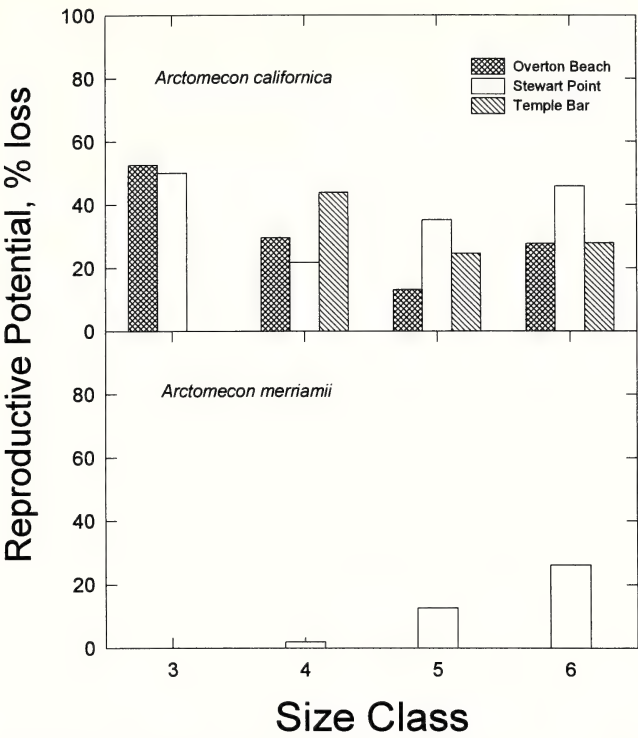


FIG. 2. Reproductive attrition (% reproductive potential lost), by size class (see Table 1), for *Arctomecon californica* (top) and *A. merriamii* (bottom) in 1993. Note: In size class 3, there was no flowering for *A. californica* at Temple Bar or for *A. merriamii*.

Reproductive attrition by reproductive stage showed a clear trend, with lower reproductive losses during flowering than at the bud and capsule stages (Table 3). This was true for *A. californica* at all three sites and for *A. merriamii*. Reproductive losses for *A. californica*

TABLE 3. REPRODUCTIVE LOSS, BY REPRODUCTIVE STAGE, FOR *ARCTOMECON CALIFORNICA* AND *A. MERRIAMII* IN 1993. Sample sizes were N = 15 (Overton Beach), N = 19 (Stewart Point), and N = 31 (Temple Bar) for *A. californica* and N = 23 for *A. merriamii*.

| Species | Site | Reproductive stage | | |
|-----------------------|---------------|--------------------|--------|---------|
| | | Bud | Flower | Capsule |
| <i>A. californica</i> | Overton Beach | 15.0 | 3.5 | 12.3 |
| | Stewart Point | 22.7 | 0.4 | 12.6 |
| | Temple Bar | 24.5 | 1.6 | 2.4 |
| <i>A. merriamii</i> | | 6.9 | 0.2 | 5.6 |

were 0 to 3% at the flower stage, 15 to 25% at the bud stage, and 2 to 13% at the capsule stage. There was a significant difference in the percentage lost at each site in each stage ($P = 0.001$ at Overton Beach, $P = 0.0001$ at Stewart Point and Temple Bar). A small proportion of the reproductive attrition for *A. californica*, 0.3% of the aborted buds and 5.3% of the aborted capsules, was due to herbivory by insects. Reproductive loss for *A. merriamii* also showed largest losses at the bud (6.9%) and capsule (5.6%) stages; flower abortion was very small (0.25%). However, these stage differences were not statistically significant ($P = 0.058$). About 15% of the aborted capsules of *A. merriamii* were due to herbivory by insects, although none of the buds were lost to herbivory.

Self-compatibility tests showed that bagged *A. californica* buds produced a lower number of seeds (3.5 ± 14) than did unbagged controls (39 ± 34 ; $P = 0.001$). Bagged buds also had a higher number of aborted seeds (89 ± 24) than did the unbagged controls (53 ± 27 ; $P = 0.0002$). Similar experiments with *A. merriamii* were less conclusive, as bagged buds had slightly, but not significantly, lower seed set (238 ± 60) than did unbagged controls (283 ± 133 ; $P = 0.52$). There was no significant difference ($P = 0.46$) in the number of aborted seeds between bagged buds (35 ± 22) and unbagged controls (67 ± 64).

Vegetation and Soils

Perennial species sampled in areas where *Arctomecon* populations were found (on-site) and in adjacent areas without *A. californica* (off-site) are shown in Tables 4 and 5. *Arctomecon californica* had the highest Importance Value (IV) on-site, except at Temple Bar, where it was second in IV to *Eriogonum inflatum*, an herbaceous perennial that preferentially occupies disturbed habitats (Table 4). In contrast, *A. merriamii* shared co-dominance with the C_4 halophytic shrub *Atriplex confertifolia* (shadscale) on both sites sampled. Off-site vegetation in the vicinity of *A. californica* populations was dominated by *Ambrosia dumosa* (bur-sage) and perennial grasses at Overton Beach, by *Eriogonum inflatum* at Stewart Point, and by *Larrea tridentata* (creosotebush) and assorted small perennials at Temple Bar (Table 4). In contrast, off-site vegetation in the vicinity of *A. merriamii* populations was strongly dominated by *Atriplex confertifolia* (Table 5). This suggests that *A. merriamii* may occupy more saline habitats than does *A. californica*. From a physiognomic perspective, *Arctomecon* sites were dominated by perennial forbs, while off-site locations were dominated by shrubs and had much greater importance of perennial grasses than did on-site locations (Tables 4 and 5).

Percent Similarity (floristic similarity) between on- and off-site

TABLE 4. IMPORTANCE VALUES OF PERENNIAL SPECIES ON SITES OCCUPIED BY *ARCTOMECON CALIFORNICA* (ON) AND ADJACENT SITES WITHOUT *A. CALIFORNICA* (OFF) AT THREE LOCATIONS IN SOUTHERN NEVADA.

| Species | Overton Beach | | Stewart Point | | Temple Bar | |
|---------------------------------|---------------|-----|---------------|-----|------------|-----|
| | On | Off | On | Off | On | Off |
| Forbs | | | | | | |
| <i>Arctomecon californica</i> | 137 | 0 | 192 | 0 | 102 | 0 |
| <i>Baileya multiradiata</i> | 0 | 3 | 0 | 0 | 0 | 0 |
| <i>Enceliopsis argophyllum</i> | 0 | 0 | 0 | 0 | 0 | 16 |
| <i>Eriogonum inflatum</i> | 0 | 3 | 15 | 122 | 107 | 60 |
| <i>Lepidium fremontii</i> | 4 | 0 | 0 | 0 | 0 | 0 |
| <i>Psathyrotes ramosissima</i> | 0 | 0 | 0 | 5 | 0 | 0 |
| <i>Sphaeralcea ambigua</i> | 0 | 3 | 0 | 4 | 0 | 54 |
| <i>Stephanomeria pauciflora</i> | 4 | 0 | 37 | 24 | 0 | 0 |
| <i>Tiquilia latior</i> | 0 | 0 | 20 | 26 | 0 | 0 |
| <i>Tidestromia oblongifolia</i> | 0 | 0 | 34 | 0 | 0 | 0 |
| Total | 145 | 9 | 298 | 181 | 207 | 130 |
| Grasses | | | | | | |
| <i>Erioneuron pulchellum</i> | 0 | 0 | 3 | 0 | 7 | 48 |
| <i>Hilaria rigida</i> | 0 | 73 | 0 | 0 | 0 | 0 |
| <i>Oryzopsis hymenoides</i> | 0 | 39 | 0 | 0 | 0 | 0 |
| Total | 0 | 112 | 3 | 0 | 7 | 48 |
| Shrubs | | | | | | |
| <i>Ambrosia dumosa</i> | 52 | 113 | 0 | 49 | 0 | 24 |
| <i>Atriplex confertifolia</i> | 34 | 0 | 0 | 0 | 0 | 0 |
| <i>Ceratoides lanata</i> | 0 | 33 | 0 | 0 | 0 | 0 |
| <i>Ephedra torreyana</i> | 58 | 15 | 0 | 0 | 10 | 0 |
| <i>Hymenoclea salsola</i> | 0 | 0 | 0 | 0 | 31 | 0 |
| <i>Krameria parvifolia</i> | 0 | 3 | 0 | 0 | 0 | 0 |
| <i>Larrea tridentata</i> | 7 | 15 | 0 | 43 | 45 | 98 |
| <i>Psoralea fremontii</i> | 3 | 0 | 0 | 28 | 0 | 0 |
| Total | 154 | 179 | 0 | 120 | 86 | 122 |

locations for *A. californica* ranged from 20 to 37% for the three sites, and from 52 to 59% for two sampled sites for *A. merriamii*. At all sites sampled (3 for *A. californica*, 2 for *A. merriamii*), there were fewer species of vascular plants on-site than off-site. Vegetation similarity analysis showed that, for *A. californica*, the Coefficient of Community (CC) between paired on- and off-site locations ranged from 0.32 at Overton Beach to 0.50 at Temple Bar (Table 6). The on-site/off-site CC averaged 0.38 for *A. merriamii*. A comparison of on-site vegetation across sites resulted in CC's of 0.29 to 0.50 for *A. californica* sites and 0.80 for *A. merriamii* sites. A comparison of off-site vegetation across sites resulted in CC's of 0.42 to 0.57 for *A. californica* and only 0.18 for *A. merriamii*. Thus paired on- and off-site locations tend to have dissimilar vegetation

TABLE 5. IMPORTANCE VALUES OF PERENNIAL SPECIES ON SITES OCCUPIED BY *ARCTOMECON MERRIAMII* (ON) AND ON ADJACENT SITES WITHOUT *A. MERRIAMII* (OFF), AT TWO LOCATIONS IN ASH MEADOWS DESIGNATED AS SITES A AND B.

| Species | Site A | | Site B | |
|---------------------------------|--------|-----|--------|-----|
| | On | Off | On | Off |
| Forbs | | | | |
| <i>Arctomecon merriamii</i> | 137 | 0 | 145 | 0 |
| <i>Enceliopsis nudicaulis</i> | 0 | 12 | 0 | 0 |
| <i>Lepidium fremontii</i> | 0 | 14 | 0 | 0 |
| <i>Psathyrotes ramosissima</i> | 0 | 15 | 0 | 0 |
| <i>Stephanomeria pauciflora</i> | 0 | 16 | 0 | 0 |
| <i>Tidestromia oblongifolia</i> | 0 | 12 | 0 | 0 |
| Total | 137 | 69 | 145 | 0 |
| Grasses | | | | |
| <i>Erioneuron pulchellum</i> | 0 | 53 | 0 | 0 |
| Total | 0 | 53 | 0 | 0 |
| Shrubs | | | | |
| <i>Allenrolfea occidentalis</i> | 0 | 0 | 0 | 61 |
| <i>Ambrosia dumosa</i> | 0 | 13 | 0 | 0 |
| <i>Atriplex confertifolia</i> | 163 | 166 | 155 | 171 |
| <i>Atriplex polycarpa</i> | 0 | 0 | 0 | 67 |
| Total | 163 | 179 | 155 | 299 |

and flora, similar to off-site locations that are significant distances apart.

Soil analyses for the three *A. californica* sites indicated that these sites had much higher levels of sulfur, calcium, and soluble salts, and much lower phosphorous contents, than did typical off-site locations that contain the dominant *Ambrosia-Larrea* vegetation type (Table 7). Total sulfur was over 10-fold higher on *A. californica* dominated sites than on adjacent off-site locations, total salts were

TABLE 6. COEFFICIENT OF COMMUNITY (CC) ANALYSES OF VEGETATION AT LOCATIONS WHERE *ARCTOMECON CALIFORNICA* OR *A. MERRIAMII* WAS PRESENT (ON) AND ADJACENT, NON-GYPSUM SITES WHERE *ARCTOMECON* WAS NOT PRESENT (OFF).

| Species | Site comparison | | | | | |
|-----------------------|-----------------|------|-----------|------|-------------|------|
| | On vs. off | | On vs. on | | Off vs. off | |
| | Site | CC | Sites | CC | Sites | CC |
| <i>A. californica</i> | OB | 0.32 | OB-SP | 0.29 | OB-SP | 0.42 |
| | SP | 0.42 | OB-TB | 0.43 | OB-TB | 0.47 |
| | TB | 0.50 | SP-TB | 0.50 | SP-TB | 0.57 |
| <i>A. merriamii</i> | A | 0.36 | A-B | 0.80 | A-B | 0.18 |
| | B | 0.40 | | | | |
| Mean | | 0.40 | | 0.51 | | 0.41 |

TABLE 7. SOIL CHEMICAL PROPERTIES FOR THREE LOCATIONS AT THE OVERTON BEACH SITE: SITES WHERE *ARCTOMECON CALIFORNICA* POPULATIONS WERE PRESENT (ON); SITES WHERE *A. CALIFORNICA* WAS NOT PRESENT (OFF); AND ADJACENT SITES THAT APPEARED TO BE GYPSUM OUTCROPS BUT DID NOT HARBOR A POPULATION OF *A. CALIFORNICA* (SIM). N = 7 for each mean value.

| Soil parameter | 0–5 cm depth | | | 6–15 cm depth | | |
|-----------------------------|--------------|------|------|---------------|------|------|
| | On | Off | Sim | On | Off | Sim |
| pH | 7.8 | 8.5 | 8.0 | 7.9 | 8.6 | 8.0 |
| Organic matter (%) | 0.31 | 0.37 | 0.29 | 0.31 | 0.38 | 0.29 |
| Soluble salts (ppm) | 2.1 | 0.53 | 2.1 | 2.3 | 0.48 | 2.3 |
| Total P (ppm) | 1.1 | 9.3 | 2.9 | 1.4 | 3.2 | 1.9 |
| NaHCO ₃ -P (ppm) | 4.9 | 12.0 | 3.7 | 4.3 | 6.5 | 4.7 |
| Ca (ppm) | 5663 | 1660 | 5207 | 5687 | 1655 | 5189 |
| S (ppm) | 999+ | 75 | 999+ | 999+ | 10 | 999+ |
| K (ppm) | 151 | 115 | 151 | 162 | 108 | 225 |
| Mg (ppm) | 39.6 | 68.2 | 58.1 | 60.0 | 64.2 | 108 |
| Na (ppm) | 13.7 | 12.3 | 13.0 | 11.9 | 11.8 | 17.6 |
| Zn (ppm) | 0.51 | 0.60 | 0.66 | 0.53 | 0.53 | 0.64 |
| Ca (% base saturation) | 97.3 | 90.1 | 96.6 | 96.7 | 90.6 | 94.6 |
| Mg (% base saturation) | 1.1 | 6.1 | 1.7 | 1.7 | 5.8 | 2.0 |
| K (% base saturation) | 1.3 | 3.2 | 1.4 | 1.4 | 3.0 | 2.0 |
| Na (% base saturation) | 0.2 | 0.6 | 0.2 | 0.2 | 0.6 | 0.3 |

TABLE 8. SOIL CHEMICAL PROPERTIES FOR A SITE AT ASH MEADOWS WITH *ARCTOMECON MERRIAMII* AND AN ADJACENT OFF-SITE LOCATION WITHOUT THE SPECIES. N = 5 for each parameter at each depth and location.

| Soil parameter | 0-5 cm depth | | 6-15 cm depth | |
|-----------------------------|--------------|----------|---------------|----------|
| | On-site | Off-site | On-site | Off-site |
| pH | 8.8 | 8.8 | 9.1 | 8.8 |
| Organic matter (%) | 1.17 | 0.98 | 1.00 | 0.92 |
| Soluble salts (ppm) | 4.3 | 0.4 | 4.8 | 0.5 |
| P (ppm) | 1.6 | 1.2 | 1.8 | 1.0 |
| NaHCO ₃ -P (ppm) | 8.8 | 9.0 | 9.4 | 8.0 |
| Ca (ppm) | 1184 | 1430 | 1164 | 1424 |
| K (ppm) | 404 | 388 | 417 | 467 |
| Mg (ppm) | 87.6 | 150 | 70.2 | 146 |
| Na (ppm) | 1272 | 357 | 1554 | 377 |
| S (ppm) | 310 | 25 | 283 | 10 |
| Zn (ppm) | 0.34 | 0.44 | 0.30 | 0.44 |
| Ca (% base saturation) | 46.7 | 65.5 | 44.0 | 64.9 |
| Na (% base saturation) | 39.5 | 14.1 | 43.7 | 13.7 |
| Mg (% base saturation) | 5.8 | 11.3 | 4.5 | 10.9 |
| K (% base saturation) | 8.0 | 9.1 | 7.8 | 8.4 |

ca. 4-fold higher on-site, and total calcium was almost 3-fold higher than for off-site locations. In contrast, total phosphorous was ca. 9-fold higher off-site than on sites with *A. californica*; off-site soils were also consistently more basic (higher pH) than on-site soils. In order to correlate soil properties between sites, each soil parameter was relativized to a grand mean for that parameter across all three sites and both depths (Table 7) prior to calculating correlation coefficients. Using this method, on-site and off-site locations were found to be strongly negatively correlated ($r = -0.89$ and -0.88 at 0-5 and 6-15 cm depths, respectively; $P = 0.0001$ for each depth). Sites near *A. californica* populations that did not support populations of the plant but had visually similar soil surface morphology (i.e., they also appeared to be gypsum outcrops) were found to have soils that were significantly similar to soils which supported *A. californica* ($r = 0.84$ and 0.72 at 0-5 and 6-15 depths, respectively; $P = 0.001$ and 0.01 for the two depths).

Many of the trends in soils found on and off *A. californica* sites were also observed for *A. merriamii* sites, but there were some important differences. Large differences in the surface layer of the soil were found between on- and off-site locations for several soil components (Table 8). The percent base saturation of sodium, as well as total sulfur content, were greater on-site, while calcium, potassium, and magnesium were greater off-site. Differences in the lower layer of soil (6-15 cm) included total calcium and the percent base saturation of calcium and magnesium being higher where *A. merriamii* was present. Sites where *A. merriamii* was present were very

different from off-site locations ($r = -0.98$ at both depths; $P = 0.0001$); surprisingly, off-site locations adjacent to *A. merriamii* populations, which are dominated by the halophyte shrub *Atriplex confertifolia*, were not higher in soluble salts than were off-site locations adjacent to *A. californica* populations. pH differences between sites with *A. merriamii* and off-site locations were negligible, but sites with *A. merriamii* populations had a subsurface pH of 9.1, versus a subsurface pH of only 7.9 for *A. californica* sites.

DISCUSSION

Mortality of both species of *Arctomecon*, *A. californica* and *A. merriamii*, was highest during the early stages of the life cycle, a pattern that typifies most desert perennials. The greatest variation in mortality for *A. californica* was observed at the Stewart Point site, where mortality in each size class was above 10% and the largest size class exhibited 38% mortality (Fig. 1). The large number of adults in this population at the beginning of the study could have been a factor in the high mortality, as these individuals could have been near the age of natural senescence. Mortality in the largest size classes of *A. merriamii* (Fig. 1) may have been due to a similar cause, as all individuals originally mapped were size class 2 or larger (Table 1), with a few extremely large individuals (size class 6). The duration of this study was too short to sort out long-term trends in population demographics for these two species, but the size structure of the populations and the high seasonal variability in plant density (Table 2) suggest that *Arctomecon* population size may be primarily driven by episodic recruitment and mortality events.

Examination of reproductive potential from a phenological stage perspective revealed that the amount of reproductive attrition at the flowering stage was quite small for both species (Table 3). This may be attributed to the fact that the time spent in the flower stage is relatively short compared to that spent in the bud and capsule stages, which may be more vulnerable to abortion events simply due to their greater development time. Reproductive attrition was greatest at the bud stage for *A. californica*, although there was also a high loss at the capsule stage. Losses were primarily due to abortion of tissues at each stage, rather than to insect herbivory. A possible explanation for the high percentage loss in the bud stage may be due to the fact that many buds were initiated later in the flowering season, when abortion may have been higher as a result of water and/or high temperature stress. Many of these late buds aborted, whereas buds initiated earlier in the spring had lower abortion rates and were in the capsule stage by the time the late buds emerged. This fits the general trend of late-maturing buds being subject to higher abortion rates than are buds that emerge earlier in the flow-

ering season (Stephenson 1981). High bud mortality can result in reduced inflorescence output, which may have a significant effect on total plant fitness. Pantone et al. (1995) found that inflorescence output was the most important reproductive attribute that resulted in reduced fitness of a rare taxon of *Amsinckia* and its widespread congener.

Although the percentage of buds lost was quite comparable across the three sites for *A. californica*, this was not the case for capsule abortion. Plants at Temple Bar showed a much smaller loss of capsules than did plants at Overton Beach and Stewart Point. This may have been due to fewer buds maturing to the capsule stage for Temple Bar plants, and thus fewer capsules to compete for limited resources from the plant on these nutrient-poor sites. Many of the capsules in each population of *A. californica* were well developed by mid-May, prior to the onset of hot, dry conditions in the summer months.

Arctomecon merriamii exhibited comparable abortion rates at the bud and capsule stages (Table 3), but these rates were much lower than for *A. californica*. This may be due to the fact that only a single bud occurs per stalk in *A. merriamii*, which may lead to higher resource supply and enhanced development per unit capsule in this species. However, it should be noted that the reproductive attrition rates in these two species of *Arctomecon* are low compared to long-lived Mojave Desert perennials such as *Larrea tridentata*, which has extremely high rates of bud, flower, and fruit abortion rates under natural conditions (Boyd and Brum 1983). It is thus noteworthy that these apparently high abortion rates cannot be implicated as a primary driving variable in the small, restricted status of *Arctomecon* populations in the region, although high bud abortion rates may result in significantly reduced total fitness in *A. californica*.

Compatibility experiments for *A. californica* showed a clear difference between the amount of seed set by buds on control plants and that set by buds unable to cross-pollinate by insect vectors; differences were also noted in the amount of seed aborted in control versus bagged buds. The Papaveraceae is thought to be a largely self-incompatible family (Faegri and van der Pijl 1979), which is supported by the results from *A. californica*. The fruit abortion data also supports the hypothesis that many fruits which are self-pollinated are more likely to abort than those which are cross-pollinated (Stephenson 1981). Compatibility experiments with *A. merriamii* did not yield as clear-cut results, however, with no significant differences observed between buds prevented from outcrossing and unbagged controls for either seed set or subsequent seed abortion. From these results it can be tentatively concluded that *A. merriamii* is able to self-pollinate when other individuals of the species are not nearby. This is logical and perhaps adaptive, considering the ecological iso-

lation of the species. It has the widest geographical range of the three species of *Arctomecon*, but it is noted for occurring in scattered clumps with few individuals in each clump. The ability to self-pollinate would obviously be advantageous in such a situation. *A. californica*, on the other hand, occurs in scattered populations over a wide area, but those populations usually consist of hundreds of individuals, often in close proximity to each other. This would favor outcrossing within each population, although each allopatric population may be genetically distinct from other populations.

Vegetation of the sites where *A. californica* and *A. merriamii* are located are visually and quantitatively different from adjacent off-site locations where *Arctomecon* is not found. As first reported for *A. humilis* (Nelson and Harper 1991), *Arctomecon* populations occur in habitats where shrub cover is much less dense than for the landscape as a whole. Common shrub species of the Mojave Desert such as *Larrea tridentata*, *Ambrosia dumosa*, and *Ephedra* spp., if found at all with *Arctomecon*, are represented by greatly diminished numbers. Lowered species diversity and cover on *Arctomecon*-dominated sites leads to a more open environment. Results for *A. californica* sites showed that off-site locations had greater community similarity to distant off-site locations than to the *Arctomecon*-dominated sites nearby. For example, the Overton Beach on/off vegetation showed a 32% community similarity to each other, but when the Overton Beach off-site vegetation was compared with off-site vegetation near the Temple Bar *A. californica* population, a 47% similarity was seen despite the sites being ca. 40 km apart (Table 6). *A. merriamii* sites tended to be highly similar in vegetation structure, consisting of large numbers of *Atriplex confertifolia* and *A. merriamii*, whereas the off-site locations had higher plant diversity and differed in community composition relative to on-site locations, even though *Atriplex confertifolia* played a dominant or co-dominant role both on- and off-site. In this regard, *A. merriamii* appears to have more similar habitat requirements to *A. humilis* than to *A. californica*, given that *A. humilis* also tends to associate strongly with *Atriplex confertifolia* (Nelson and Harper 1991). However, *A. merriamii* is apparently not a gypsophile over its entire distributional range, whereas *A. californica* and *A. humilis* are (personal observations). Even so, when taken together these results indicate that the vegetation on *Arctomecon*-dominated sites is quite different from off-site vegetation, which remains somewhat similar over great distances in the Mojave Desert.

Quantitative analysis of soils on and off *Arctomecon*-dominated sites showed that sites which support *Arctomecon* populations have much higher total sulfur and soluble salt contents, and lower magnesium, than off-site locations (Tables 6, 7). High sulfur levels where *Arctomecon* was present, which are characteristic of gypsum-

dominated soils, may have an effect on establishment of new plants, as sulfur content has been hypothesized to be an important factor in the establishment and success of certain species on gypsum soils (Parsons 1976). On sites which supported *A. californica*, soils contained lower phosphorous and magnesium levels and higher calcium and soluble salt levels than off-site (Table 6). Sites which supported *A. merriamii* populations showed much higher values of sodium and sulfur, and lower concentration of magnesium, than off-site locations (Table 7). Although these analyses point to strong differences in soil chemistry between *Arctomecon*-dominated and off-site locations, it has been proposed by Meyer (1986) that the important factor allowing some species to establish on gypsum soils but not others is due to surface effects of the soil, not to chemical factors per se. An important factor relative to the establishment of *Arctomecon* and other taxa on these soils may be the presence or absence of cryptogamic crusts. Many *Arctomecon*-dominated sites in southern Nevada, particularly sites with *A. californica*, can have an almost continuous cover of these surface crusts. Similarly, sites dominated by *A. humilis* in Utah exhibit a mean 84% cryptogamic crust cover (Nelson and Harper 1991). Cryptogamic crusts have been shown to increase nutrient levels in the top layer of soil (Harper and Pendleton 1993), which may be a factor in the success of *Arctomecon* on gypsum soils. They also strongly influence infiltration of rainfall, and thus influence surface water balance, and may also protect the often "fluffy" soils of gypsum outcrops from wind erosion.

Although a descriptive preliminary study such as this cannot conclusively determine what attributes of gypsum outcrops result in the apparent narrow edaphic requirements of *Arctomecon* to gypsum soils, it is clear that the imbalance in soil chemistry relative to off-site locations allows these plants to occur on sites where most other species apparently cannot become established. However, results for *A. merriamii* may be site specific, as this species has also been located on limestone outcrops, so its soil requirements may be more broad than for *A. californica* or its soil requirements may vary across its distribution. Further research needs to be conducted on the edaphic requirements of *A. merriamii*, as it is the most widely distributed of the three species of *Arctomecon*, but occurs in low density populations.

Soils were compared between sites that support *A. californica* and sites that did not support the species but appeared similar edaphically (i.e., were gypsum outcrops). Comparisons indicated that these two types of sites were highly correlated, and thus similar in soil structure and chemistry. Although this analysis may have failed to identify an important, but subtle, soil factor that limits the expansion of *A. californica* onto these sites, it does lead to the possibility that the local distribution of *A. californica* may not be based on soil

requirements alone (indeed, sites in Utah that support populations of *A. humilis* show pronounced variability in several important soil parameters; Nelson and Harper 1991). A similarity in soils between occupied and closely adjacent non-occupied sites may also lead to the hypothesis that the establishment of *A. californica* on the non-occupied site has not yet taken place (i.e., the population could be expanding), but is a distinct possibility for the future. If so, these areas with no existing *Arctomecon* populations but with similar soils should be considered candidates for preservation as possible habitat that the species may utilize in the future. Alternatively, these sites with similar soils may have once supported *Arctomecon* populations, which have since contracted to more localized populations. This possibility would also argue for preservation of these sites with similar soils if the goal of management programs is to increase *Arctomecon* populations in the future, particularly if the proximate causes for contraction of *Arctomecon* populations are primarily related to anthropogenic disturbance.

Important management conclusions that can be drawn from this study include the observation that most of the mortality in *Arctomecon* populations occurs in the seedling stage, which is potentially important since the seedling stage is the precursor for future adult populations (Palmer 1987). Although almost all desert perennials exhibit highest mortality in the seedling stage, this becomes more important for the management of potentially endangered species such as *Arctomecon*. Since areas with many seedlings, for both *A. californica* and *A. merriamii*, will probably experience a high degree of mortality, it is essential that these populations be managed with care so that the few plants that survive to reproductive age can replenish the seed bank. Also, apparently not all habitat which is available is being utilized, as indicated by the soil analyses. Conservation of unoccupied, but similar, habitat is important for long-term conservation of the species, especially *A. californica*, whose habitat is continually encroached upon by urban development and ORV use. Since these edaphically-similar sites are usually adjacent to *Arctomecon* populations, protection of these sites would also provide needed buffer area for the existing populations.

In conclusion, high mortality of *Arctomecon* seedlings is considered a potential bottleneck in the preservation of both species. Reproductive attrition per se does not seem to be a critical factor in the survivorship of populations of either species. Isolation of *A. californica* plants could be highly detrimental to seed set, while such a situation does not appear detrimental to the more self-compatible *A. merriamii*. Preservation of unoccupied, but edaphically similar, habitat may be the best method of species preservation at this time. Currently, the relatively large geographical distribution of *A. merriamii* and its isolation from urban development leads to the con-

clusion that it is not in as great of a danger of extinction as is *A. californica*.

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FACTORS INFLUENCING THE PROBABILITY OF OAK REGENERATION ON SOUTHERN SIERRA NEVADA WOODLANDS IN CALIFORNIA

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ABSTRACT

Regeneration of oaks on California's 3.0 million hectares of hardwood rangelands has been identified as a critical factor affecting the sustainability of this important source of biological diversity in the state. A survey of oak seedling and sapling regeneration was carried out in the southern Sierra Nevada region of the state on 192 sample plots. Logit regression analysis was carried out on vegetation and site factors to predict the probability of finding any seedling (trees less than 0.3 m in height) or sapling (trees between 0.3 and 3.0 m in height) oak regeneration on sample plots. Oak regeneration probability relationships were derived for *Quercus douglasii* Hook. & Arn. (blue oak), *Q. wislizeni* A. DC. (interior live oak) and *Q. crysolepis* Liebm. (canyon live oak), and *Q. kelloggii* Newb. (black oak). Tree cover was found to be positively correlated with the probability of seedling and sapling regeneration for all three species groups. Grazing was negatively correlated with *Q. douglasii* seedling probability, and nonsignificant with *Q. douglasii* saplings or the other species evaluated. Solar radiation levels derived from site slope and aspect were significant factors for *Q. kelloggii*, *Q. wislizeni*, and *Q. crysolepis* seedlings. Elevation was positively related to the probability of finding *Q. douglasii* seedlings. These relationships can be used by managers of hardwood rangelands to prioritize restoration efforts, grazing management, and other site treatments to ensure the long-term sustainability of the hardwood rangeland resource.

California's oak woodlands, also known as hardwood rangelands, occupy an estimated 3.0 million hectares (Bolsinger 1988). These oak woodland areas are characterized by an overstory canopy of at least ten percent hardwood tree species, predominantly in the genus *Quercus*, with an understory of annual grasses and occasional native perennial grasses. Griffin (1978), Bartolome (1987), Holmes (1990), and Allen et al. (1991) provide good ecological descriptions of these areas.

Since European settlement of California, oak woodlands have

been managed primarily for livestock production (Huntsinger and Fortmann 1990). These areas have taken on a new importance because of the recognition that they have the richest wildlife species abundance of any habitat in the state, with 331 vertebrate species relying at least partly on oak woodlands (Verner 1980; Barrett 1980). Other public values obtained from these areas include water quantity and quality, outdoor recreation, and aesthetics. California's oak woodlands are somewhat unique for western wildlands, with over 80% in private ownership (Bolsinger 1988).

Because of the significant ecological values supplied by hardwood rangelands, sustainability of these oak dominated habitats has great importance. To maintain stands at current canopy density, sufficient oak regeneration must be present to replace mature trees lost to mortality. Maintenance of remaining oak stands is especially critical, since the total area of oak woodlands has decreased by about 485,000 ha since 1945 (Bolsinger 1988) due to clearing for urbanization and intensive agricultural production.

Concern about the lack of regeneration for some oak species has been evident in the literature. Sudworth's (1908) early description of California's trees noted the apparent poor natural regeneration of several oak species, especially *Q. douglasii* Hook. & Arn. (blue oak). White (1966) documented the lack of trees in the sapling size class in oak woodlands on California's central coast and raised concerns about the long-term sustainability of these areas. Griffin (1977) noted a lack of young oak seedlings and hypothesized that this might be due to livestock grazing, rodent herbivory, and the introduction of annual exotic plants into the understory. Gordon et al. (1989) evaluated *Q. douglasii* seedling moisture competition with exotic annual grasses and perennial native grasses and demonstrated that current conditions are more xeric than presettlement times. Allen-Diaz and Bartolome (1992) evaluated natural *Q. douglasii* seedling establishment, survival, and growth in north coastal California oak woodlands and concluded that *Q. douglasii* has a successful strategy for seedling establishment. However, their research was not able to determine the factors which prevented recruitment of seedlings to the sapling size class. Fire and sheep grazing were eliminated as factors inhibiting sapling recruitment. Borchert et al. (1989) found very low seedling recruitment in *Q. douglasii* woodlands on the central coast of California due to herbivory from a variety of rodents and ungulates.

Recent statewide surveys of California's oak woodlands carried out by Bolsinger (1988) and Muick and Bartolome (1987) also confirm that the absence of oak saplings, especially *Q. douglasii* and *Q. lobata* Nee (valley oak), may make sustainability of the resource difficult in some areas.

OBJECTIVE

Managers of hardwood rangelands must be able to assess the likely occurrence of seedlings or saplings on a given site to assess sustainability of the resource. For example, if very low occurrence of oak seedlings was observed on a site with high mortality of mature overstory oaks, then it would be important for managers to design artificial oak regeneration plans to maintain oak cover over time. If there was a high probability of oak seedlings being present on a site, but a low probability for saplings, then managers would need to design regeneration strategies to protect seedlings from factors which impede recruitment to the sapling size class.

The objective of this study was to develop models to predict the probability of oak regeneration on specific hardwood rangeland areas. Particular emphasis was given to evaluating the factors which contribute to the presence or absence of oak regeneration on a given site.

The information presented will help provide an initial assessment of potential sustainability of the hardwood range resource and help guide managers in identifying critical hardwood range habitat where intervention may be necessary to ensure that regeneration occurs.

STUDY AREA

A four-county area in the western foothills of the southern Sierra Nevada range in California was chosen for this study. This region, consisting of Madera, Fresno, Tulare, and Kern counties has almost 620,000 ha of hardwood rangelands, which is about 20% of the total hardwood rangeland area in the state. The northern extent of the sample area was at a latitude of 37°12'N, northeast of the city of Fresno. The southern extent of the sample area was at a latitude of 35°30'N, east of the city of Bakersfield.

There are five principal oak species found in the southern Sierra Nevada hardwood rangelands. *Quercus kelloggii* Newb. (black oak) is found from higher elevation mixed-conifer forest sites down to moister sites in the hardwood range region. *Quercus lobata* is found in riparian zones, in deep alluvial soils, and on moist hillsides. *Quercus wislizeni* A.DC. (interior live oak) and *Q. crysolepis* Liebm. (canyon live oak) grow in dense clusters on moist sites. *Quercus douglasii* is found at the lower edge of the hardwood range land area before it becomes open grassland, quite probably due to moisture limitations, and also in mixed-woodland stands with the other *Quercus* species listed above. Other principal associated tree species present include *Pinus sabiniana* Douglas (foothill pine) and *Aesculus californica* (Spach) Nutt. (California buckeye).

METHODS

A series of ten major oak regeneration transects was established on both private rangeland and USDA Forest Service lands, beginning at an elevation with sufficient rainfall to support open *Q. douglasii* savanna cover, about 180 m in the northern part of the sample area and 485 m in the most southern part of the sample area. The upper elevation for the sample transects was the transition zone between oak woodlands and mixed conifer forest, which occurred at about 920 m elevation in the northern region of the study area and 1525 m in the southern part.

A total of 192 survey plots were randomly located 60 m to the north or south of the main elevational transects. Random plot locations were checked to ensure that they occurred in the oak woodland vegetation type. If a plot was not in oak woodlands, then another location was randomly selected.

At each sample location, a strip transect, 30.5 m long and 3.7 m wide was laid out (0.011 ha) in a randomly chosen direction. Data were collected during the months of July and August in 1987, 1988, and 1989. The diameter at breast height (DBH), 1.4 m above the ground, and total height were taken for each overstory tree in the plot, defined as trees with DBH over 2.5 cm. This was used to calculate overstory basal area, number of trees, and volume per ha. Tree and shrub crown cover by species was recorded at each plot using a line intercept sampling method. Herbaceous plant residual dry matter was estimated as high, medium, or low (greater than 800, 550, and less than 400 kg/ha respectively) using visual comparisons with known standards (Clawson et al. 1982). Slope, aspect, elevation, and whether there was livestock grazing were recorded for each site. Species, height, and root collar diameter were recorded for all oak under 3 m in height. Oak trees less than 0.3 m in height were classed as seedlings, and trees from 0.3 m to 3 m in height were classed as saplings.

To assess oak seedling and sapling regeneration probability, a dummy variable, STOCK, was set to zero if there was no oak regeneration on the site, that is, the plot was unstocked. The site was considered to be stocked with seedlings or saplings if there was at least one tree in either of these classes on the sample plot, representing at least 90 seedlings or saplings per hectare. The value of STOCK for stocked sites was set to one. Species type was considered in assigning the value to STOCK. For example, if a mixed stand had an overstory with both *Q. douglasii* and *Q. kelloggii*, and seedlings of *Q. kelloggii* were present but seedlings of *Q. douglasii* were not, then the value of STOCK would be set to one for *Q. kelloggii* and to zero for *Q. douglasii*.

This measure of regeneration, i.e., present or absent, is somewhat

crude. It merely serves as a preliminary estimate of whether seedlings or saplings are likely to be present or absent from a site. This information would need to be combined with observations of over-story mortality as well as a quantitative account of the distribution of trees by size class to determine if there is a regeneration problem for a given site. This first cut at evaluating the site factors will help managers to evaluate where to concentrate efforts, and to evaluate where more detailed stand structure data collection should be emphasized.

This study hypothesized that sample plot regeneration stocking was a function of abiotic site factors such as rainfall and solar insolation, vegetation characteristics such as competition from over-story trees, shrubs, grasses, and forbs, and management factors such as grazing history or fire frequency. The predicted value of the dependent variable, STOCK, can be interpreted as the probability of a site being stocked.

(1) STOCK = f(abiotic site factors, vegetation, management).

Since the dependent variable, STOCK, is a discontinuous variable having a value of either 0 or 1, normal regression procedures to evaluate hypothesized explanatory variables could not be used. For such data, the assumptions implicit in ordinary least squares solution of linear regression are violated, and it is possible that a resulting predictive equation could give a value for the dependent variable outside the 0 to 1 range. The common practice in this situation is to transform the dependent variable using the logistic function, a process known as *logit* regression. This procedure utilizes a maximum likelihood estimation process to estimate the coefficients for the independent variables in the prediction equation shown in (2). A complete discussion of the assumptions of logit regression are given in Wonnacott and Wonnacott (1979).

$$(2) \quad \text{STOCK} = \frac{1}{1 + e^{-(x'\beta)}}$$

β = vector of logit regression
coefficients

x = vector of independent variables.

Separate logit analyses were carried out on the probability of a site being stocked with seedlings and saplings for each oak species in the study. The independent variables evaluated are described below. Independence of variables was ensured through observation of the correlation matrix of the variables.

Solar radiation—The site factors of slope and aspect were combined into a single variable for the amount of solar radiation reaching

TABLE 1. SUMMARY OF 192 OAK REGENERATION PLOTS IN SOUTHERN SIERRA NEVADA SAMPLE.

| <i>Quercus</i> species | Regeneration category | Percentage of stocked plots |
|--|-----------------------|-----------------------------|
| <i>Q. douglasii</i> | Seedling | 64 |
| | Sapling | 31 |
| <i>Q. kelloggii</i> | Seedling | 83 |
| | Sapling | 25 |
| <i>Q. wislizeni</i> and <i>Q. crysolepis</i> | Seedling | 75 |
| | Sapling | 48 |

the site, expressed in calories per day per square centimeter following the procedure in Buffo et al. (1972). June 22nd was selected as the date for calculating solar radiation since day length is longest and the sun is at its highest on that date, representing the maximum evaporative demand on the site.

Elevation in meters—Rainfall in the southern Sierra Nevada increases with elevation (Standiford et al. 1991), and this factor is a proxy for the annual rainfall at the site.

Grazing—A dummy variable for the presence (grazing = 1) or absence (grazing = 0) of grazing.

Number of woody species on site—The diversity of woody species at the site is affected by a variety of abiotic and biotic factors. In general, the diversity of woody species increases as the amount of available moisture at the site increases due to rainfall and soil characteristics.

Shrub crown cover percent—Individual cover by species was collected and combined to give total shrub cover on the site.

Tree cover—Total crown cover for all trees was evaluated, as well as the cover of individual *Quercus* species.

Forage residual dry matter—A dummy variable with 3 = high, 2 = medium, 1 = low.

RESULTS

Table 1 summarizes the information collected from sample plots. On the 192 survey plots, *Q. douglasii* was the most common species in these southern Sierra Nevada oak woodlands, occurring on 131 plots. *Q. kelloggii*, *Q. wislizeni*, and *Q. crysolepis* cover were present on about one-third of the plots sampled. Seedlings were fairly commonly found for all *Quercus* species. About 64% of the plots with *Q. douglasii* overstory cover were stocked with *Q. douglasii* seedlings, which meant there was at least one seedling present in the plot. *Q. kelloggii* seedlings were found on 83% of the plots with *Q. kelloggii* cover, while 75% of the plots with either *Q. wislizeni* or *Q. crysolepis* cover had seedlings for these species. A smaller per-

centage of plots were stocked with sapling oaks, ranging from 25% stocking for *Q. kelloggii* to 48% stocking for *Q. wislizeni* or *Q. crysolepis* plots.

Table 2 shows results of the logit regression of the independent variables on probability of oak seedling or sapling stocking. All coefficients shown were significant at the 0.10 level using a t-test. The significance of the entire equation was evaluated using the Chi-square statistic to test the hypothesis that

$$(3) \quad b_0 = b_1 = b_2 = \dots = b_i = \dots = b_n = 0$$

where b_i = logit coefficient.

This hypothesis was rejected at the 0.05 level of significance for the six equations in Table 2. The percentage of plots correctly classified with the logit regression equations as to the presence or absence of oak regeneration are also shown. Prediction success ranged from 61% of the *Q. wislizeni* and *Q. crysolepis* sites correctly classified as stocked or unstocked with saplings, to 83% of the *Q. kelloggii* sites classified as stocked or unstocked with seedlings.

An example of use of the logit coefficients in Table 2 to predict the probability of *Q. douglasii* seedlings on an area with 30% total overstory tree cover, elevation of 900 m, and livestock grazing is

$$(4) \quad \text{STOCK} = \frac{1}{1 + e^{-[-0.789 + 0.00156(900) - 1.487(1) + 0.0232(30)]}}$$

$$= 0.456.$$

This means that for these site factors, there is about a 46% probability that the area will be stocked with *Q. douglasii* seedlings.

DISCUSSION

Seedling and sapling stocking in this study were compared with similar data from Bolsinger's (1988) statewide oak regeneration survey. In general, this southern Sierra area had a higher probability of seedling regeneration and lower probability of sapling regeneration than the statewide averages in Bolsinger (1988). The individual species are discussed below.

QUERCUS DOUGLASII. *Quercus douglasii* is the most widespread oak woodland cover type in the California. In this study, elevation, livestock grazing, and tree canopy cover were significant independent variables to predict *Q. douglasii* seedling stocking. The effects of grazing, elevation, and tree canopy cover on *Q. douglasii* seedling regeneration probability is shown in Figures 1 and 2 derived from the logit regression analyses. On dry, low elevation sites, and also on oak savannas with low canopy cover, there is a low probability

TABLE 2. LOGIT COEFFICIENTS FOR ESTIMATING THE PROBABILITY OF *Q. DOUGLASII*, *Q. KELLOGGII*, *Q. WISLIZENI* AND *Q. CRYSOLEPIS* SEEDLING AND SAPLING STOCKING. Numbers in parentheses are t-values for the coefficient. Significance of t-values are ***—significant at $P < 0.01$; **—significant at $P < 0.05$; *—significant at $P < 0.10$.

| Variable | <i>Q. douglasii</i> | | <i>Q. kelloggii</i> | | <i>Q. wislizeni</i> and <i>Q. crysolepis</i> | |
|-----------------------------|----------------------|----------------------|---------------------|---|--|----------------------|
| | Seedling | Sapling | Seedling | Sapling | Seedling | Sapling |
| Constant | -0.789 [-1.42]* | -2.189 [-3.52]*** | 7.8902 [1.34]* | -3.0194 [1.88]** -0.00425 [-1.41]* | -6.108 [-2.53]*** | -0.8699 [-2.27]** |
| Elevation | 0.00156 [2.97]*** | | | | | |
| Solar radiation | | | -0.0109 [-1.43]* | | 0.0077 [2.43]*** | |
| Graze | -1.487 [-2.98]*** | | | | | |
| Total tree cover | 0.0232 [2.64]*** | | | | | |
| <i>Q. douglasii</i> cover | 0.0173 [1.80]** | | | | | |
| <i>Q. kelloggii</i> cover | | | 0.0516 [2.93]*** | 0.0316 [2.70]*** | | |
| Live oak cover ¹ | | | | | 0.0256 [1.47]* 0.0429 [2.19]** | 0.0325 [2.62]*** |
| Non-target tree cover | | | | | | |
| No. woody species | | 0.315 [2.19]** | | | | |
| Equation significance | *** | | *** | *** | *** | *** |
| Pct. right predictions | 0.748 | 0.718 | 0.828 | 0.756 | 0.803 | 0.607 |

¹ Includes *Q. wislizeni* and *Q. crysolepis*.

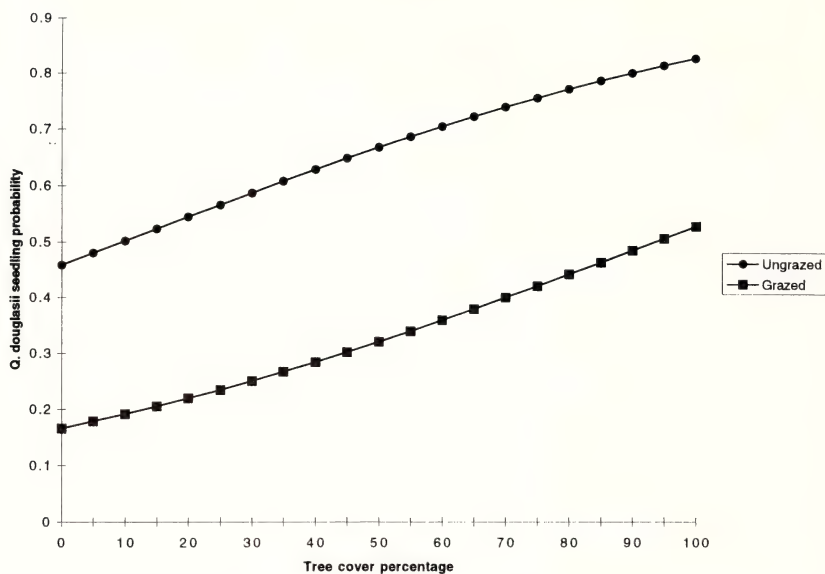


FIG. 1. Probability of *Q. douglasii* seedling regeneration in southern Sierra Nevada oak woodlands at 900 m elevation with varying overstory tree cover.

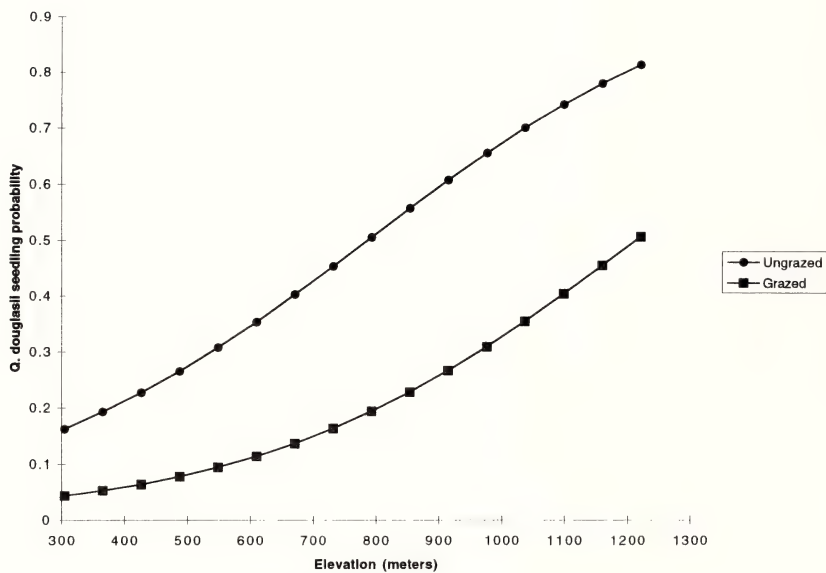


FIG. 2. Probability of *Q. douglasii* seedling regeneration in southern Sierra Nevada oak woodlands with 35% tree cover with varying elevation.

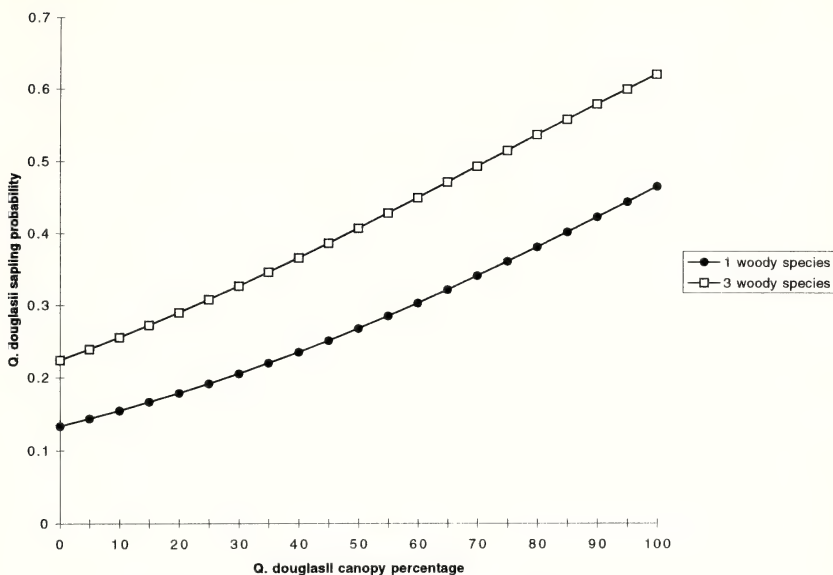


FIG. 3. Probability of *Q. douglasii* saplings in southern Sierra Nevada oak woodlands by *Q. douglasii* canopy cover and the number of woody species on the site.

of stocking with *Q. douglasii* seedlings. A negative grazing effect on seedling probability is also demonstrated. Hall et al. (1992) have shown how livestock season of use and grazing intensity influences *Q. douglasii* seedling herbivory and suggest grazing strategies to minimize these losses. Borchert et al. (1989) also demonstrated lower *Q. douglasii* seedling recruitment in grazed areas. This can be contrasted with the results by Allen-Diaz and Bartolome (1992), which showed that typical sheep grazing in coastal *Q. douglasii* woodlands had no effect on seedling establishment or mortality when compared to ungrazed areas.

In general, there were a low number of *Q. douglasii* saplings in this survey. The probability of *Q. douglasii* saplings on a site increases as *Q. douglasii* cover and the number of woody species present increases. Bolsinger (1988) also found a high correlation with *Q. douglasii* regeneration and the number of woody species on a site. Figure 3 graphically shows the *Q. douglasii* sapling probability curve for tree cover and woody species present. On pure *Q. douglasii* stands with low canopy cover, sapling stocking probability is low. As woody species diversity increases, the probability of saplings increases.

Given these relationships, it is clear that managers will often need to implement practices designed to increase recruitment into the sapling size class to ensure sustainability of *Q. douglasii* cover types.

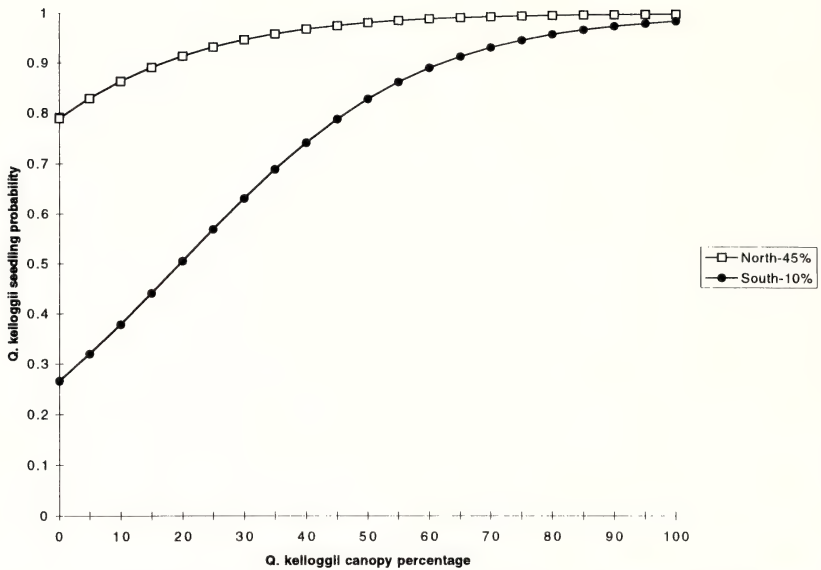


FIG. 4. Probability of *Q. kelloggii* seedling regeneration in southern Sierra Nevada oak woodlands for two slopes and aspect classes with varying *Q. kelloggii* cover.

This is most pronounced on low elevation savanna sites where *Q. douglasii* is the only woody species present.

QUERCUS KELLOGGII. To date, there has not been much concern expressed about *Q. kelloggii* regeneration in the state, as *Q. kelloggii* cover has increased in recent years (Bolsinger 1988). Much of this increase has taken place due to conversion of conifer forest lands as a result of silvicultural practices that favor conifer harvest over *Q. kelloggii* harvest. Little study has been made of oak woodlands with a *Q. kelloggii* component. The southern Sierra Nevada is a major area where *Q. kelloggii* occurs in woodlands. This study showed a very high probability of *Q. kelloggii* seedling stocking influenced by the amount of solar radiation (combination of slope and aspect) and the amount of *Q. kelloggii* tree cover. As solar radiation increases, *Q. kelloggii* seedling probability decreases. This may indicate that *Q. kelloggii* is not tolerant of the high evapotranspiration resulting from high solar insolation. Figure 4 shows seedling probability for different *Q. kelloggii* cover percentages at two solar radiation levels. Dry south slopes with low *Q. kelloggii* canopy cover have the lowest probability for seedlings.

This study shows a very low sapling component in *Q. kelloggii* stands, with only 25% of the plots having saplings. This is consistent with the classification of *Q. kelloggii* as a shade-intolerant species

(Burns and Honkala 1990). The relatively high canopy cover for stands with a *Q. kelloggii* component in this study (67%) may result in poor recruitment of seedlings to saplings due to competition with overstory trees for light and moisture. This study shows that managers need to carefully assess the rate of mortality for mature *Q. kelloggii* trees, as the low sapling probability on some sites may lead to an eventual decline in cover. It may be necessary to develop management practices to enhance seedling recruitment into the sapling class.

QUERCUS WISLIZENI AND *Q. CRYSOLEPIS*. This study showed that *Q. wislizeni* and *Q. crysolepis* seedlings and saplings have a fairly high probability of occurring, with 75% of the *Q. wislizeni* and *Q. crysolepis* plots having seedlings and 48% having saplings. Regeneration probability was not shown to be significantly related to grazing or elevation. The lack of significance of elevation is probably because *Q. wislizeni* and *Q. crysolepis* occurred over a relatively narrower range than either *Q. douglasii* or *Q. kelloggii*. Solar radiation had a significant positive relationship with the probability of seedling stocking. *Q. wislizeni* and *Q. crysolepis* with their sclerophyllous leaf anatomy is more drought tolerant than *Q. douglasii*, and might be predicted to dominate on sites with higher solar radiation.

CONCLUSIONS

Our study identified factors associated with the probability of *Q. douglasii*, *Q. kelloggii*, *Q. wislizeni*, and *Q. crysolepis* regeneration in southern Sierra Nevada oak woodlands. In general, there was a relatively high probability of oak seedling stocking in most areas. However, oak seedlings may not persist in the landscape for the long term. Allen-Diaz and Bartolome (1992) have shown that annual mortality of natural *Q. douglasii* seedlings is about 50% per year for several years. Relatively low probability of sapling stocking in this study suggests there may be a problem in having adequate recruitment of oaks to replace mortality of mature trees. Oaks in the sapling height class are usually well established, and have a high probability for remaining in the landscape to replace mature trees lost to mortality, so it is the probability of saplings that has the greatest effect in oak woodland sustainability.

In our study, a significant grazing effect was detected only for *Q. douglasii* seedlings. Future work can perhaps determine if grazing strategies, such as those suggested by Hall et al. (1992), can increase *Q. douglasii* sapling recruitment from the relatively more abundant seedlings found in this study.

In areas with low seedling and sapling probability, it may be necessary to intervene with management practices, such as preparation of a seed bed with fire or weed control, protection against

insect or rodent herbivory, or modification of season and intensity of livestock grazing, to ensure recruitment of seedlings into the sapling class. The probability relationships derived in this study can be used to help identify and concentrate management and protection efforts needed. In particular, seedling and sapling probability curves can be used to guide decisions about the need for artificial oak regeneration. Planting oak seedlings or direct seedling of acorns can be concentrated on those areas with the lowest probability for natural regeneration.

Overstory tree cover was positively correlated with the probability of oak seedlings and saplings. This suggests that in very open oak savannas, where the probability of seedlings and saplings is lower than in dense woodland stands, overstory thinning may result in a stand with an inadequate number of saplings to replace thinned trees. There is insufficient information in this study about the cause-effect relationship between oak canopy and regeneration to determine if thinning in denser stands might release seedlings or saplings for recruitment into larger size classes. Our study found a range of tree covers from 0 to 100%, with a mean of 54%.

The relationships developed in our study can be coupled with mortality estimates (Swiecki et al. 1991) and tree growth estimates (Standiford and Howitt 1988) to assess current management practices, and the likelihood that oak stands can be sustained and continue to provide ecological benefits for future generations.

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**ATRIPLEX SUBTILIS (CHENOPODIACEAE): A NEW SPECIES
FROM SOUTH-CENTRAL CALIFORNIA**

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ABSTRACT

Atriplex subtilis, sp. nov., is a newly described species from south-central California. It is a short-statured, fine-textured, diploid annual, with opposite leaves and branches. Its leaves are small (ca 2–4 mm long, 1.5–3 mm wide), cordate and sessile. It is morphologically most like *A. depressa* Jepson but differs from *A. depressa* in several characteristics, including shape of fruiting bracts (deltoid instead of rhomboid), position and arrangement of fruiting-bract appendages (both sides instead of adaxial side only), more slender stems, and longer internodes. *A. subtilis* is confined to south-central California, mostly in Tulare, Fresno, Kern, and Kings counties; *A. depressa* occurs in more northerly latitudes, primarily in Glenn and Yolo counties.

***Atriplex subtilis* Stutz & G.L. Chu, sp. nov. (Fig. 1). —TYPE:**
USA, California, Kings Co., 12 miles W of Tulare, SE corner
of Kansas Avenue and 6th Avenue, T20S R22E S4, 30 Aug.
1994, *H. C. Stutz 9654* (holotype, BRY).

Herba annua, 10–30 cm alta. Caulis erectus, multi-ramosus; rami graciles, teres, absque striaque costis; medii et inferi ramuli fere oppositi, oblique patuli, saepe purpureo-rubelli, dense furfuracei, internodiis 5–15 mm longis, 0.6–1.2 mm diam. Folia sessilia, plerumque fere opposita, ovato-deltoides usque lato-ovata, polio-viridia, 2–4 mm longa, 1.5–3 mm lata, saepe patentia, apice obtusa, base cordata, amplexicaulia, integra, utrinque dense fufuracea. Stamina et pistillati flores mixti in glomerulos, axillares ad lotos ramos; perianthium staminalis floris depresso-globosum, 1–1.5 mm diam., plerumque 4- raro 5-partium usque prope basin; segmenta ovata ca. 1 mm longa, membranacea, leviter carnosa dorsaliter prope apices; stamina tot quot segmenta perianthiorum, filamentis ca. 1.5 mm longis et oblongis antheris 0.3–0.5 mm longis. Fructiferae bractae sessiles, deltoideae ca. 3 mm longae et latae, apice brevi-acuminatae, margine 1–3 paribus dentium, basale par dentium saepe magnius et deorsum patens, plerumque utrinque distichis longitudinaliter tuberculiformibus appendicibus. Utriculus suborbicularis, ca. 1.2 mm diam., membranceo pericarpio. Semen atro-brunneum duro perispermio, radícula supra.

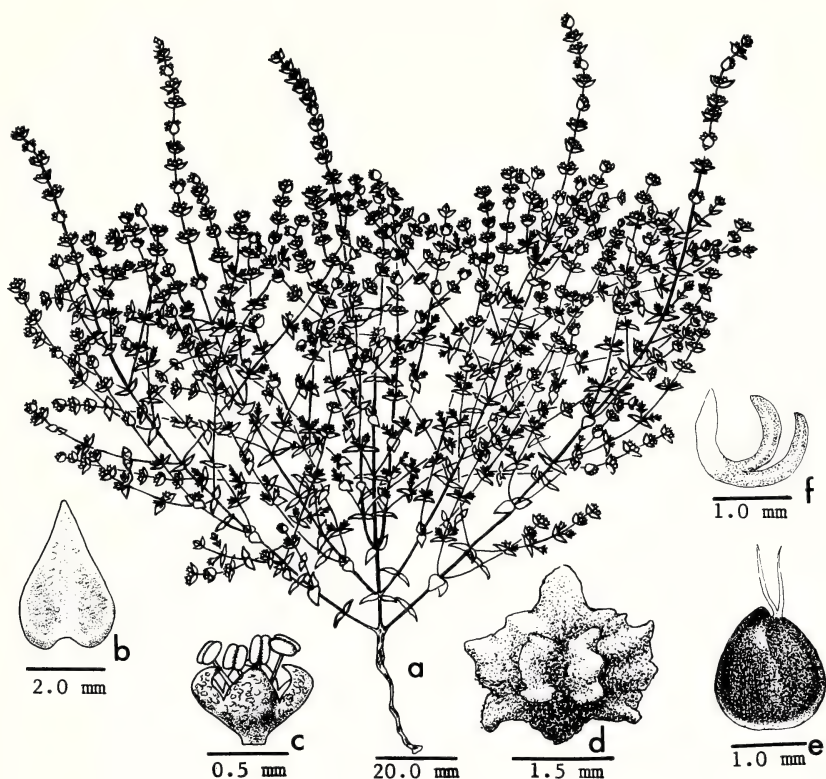


FIG. 1. *Atriplex subtilis*. a. Habit. b. Leaf. c. Male flower. d. Fruiting-bract. e. Utricle. f. Embryo. (Drawings of a,b,c by Loretta Orgill; d,e,f by Marcus A. Vincent.)

Annual herb, 10–30 cm tall. Stem erect, much-branched, slender, terete, 0.6–1.2 mm in diam., not ribbed nor striate; branchlets opposite, occasionally alternate in upper branchlets, oblique-spreading, usually purple-reddish, densely furfuraceous; internodes 5–15 mm long. Leaves sessile, mostly opposite, ovate-triangular to broad-ovate, 2–4 mm long, 1.5–3 mm wide, mostly clasping and spreading, grey-green, apex obtuse, base cordate, entire, densely furfuraceous on both surfaces; Kranz-type venation. Male and female flowers mixed in glomerules, axillary throughout nearly all branches; perianth of staminate flowers depressed-globose, 1–1.5 mm in diam., usually 4-parted, rarely 5-parted to near base, segments ovate, ca. 1 mm long, membranaceous, slightly fleshy dorsally, near apex; stamens as many as perianth segments, filaments ca. 1.5 mm long, slightly exerted in flowering, anthers orange-red, short-oblong, 0.3–0.5 mm long; rudimentary pistil columnar; fruiting bracts sessile, deltoid, ca. 3 mm long and wide, apex short-acuminate, margin ir-

regular with 1–3 pairs of teeth, the two basal marginal teeth usually larger and downward spreading, with 2 longitudinal rows of tuberculate appendages on both surfaces of bracts or rarely, only on adaxial surface. Utricle suborbicular, ca. 1.2 mm in diam., pericarp membranaceous. Seed dark-brown, with solid perisperm; radicle superior.

Chromosome number: $2n=18$ (determined from anthers fixed and stored in 5% acetic acid and squashed in aceto-carmin stain).

Flowering and fruiting period: August–October.

Paratypes. USA, California, Fresno Co.: 8 mi W of Karman, 10 Aug 1937, *R. F. Hoover 2655* (UC); State highway 180, 0.6 mi E of junction of road southward to Jameson siding and Tranquility, 9 Nov 1962, *R. Bacigalupi & L. R. Heckard 8776* (UC, RM). Kern Co.: 10 mi W of Shafter, 29 Aug 1989, *H. C. Stutz 95144* (BRY); 10 mi W of Shafter, Lerdo Highway, then S $\frac{1}{4}$ mile, 28 Aug 1994, *H. C. Stutz 9649* (BRY); Rowlee Rd., 1 mi N of Lerdo highway, 5 Aug 1995, *H. C. Stutz 9783* (BRY). Madera Co.: 4 mi SW of Chowchilla, 1 Oct 1936, *R. F. Hoover 1613* (UC). Merced Co.: 12 mi E of Dos Palos on Chowchilla Road, 11 Oct 1921, *H. M. Hall 11756* (UC); El Nido, 1 Oct 1936, *R. F. Hoover 1597* (UC). Tulare Co.: Visalia, Oct 1881, *Jepson* (CAS); Goshen, about R.R. station, 1 Sep 1905, *K. Brandegee* (UC); 40-acre vernal pool area, $\frac{1}{4}$ mi N of Ave. 104, Road 124, 3 Aug 1963, *E. McClintock* (CAS); 40-acre pool area near Pixley, $\frac{1}{4}$ mi N of Ave. 104, Road 124, Sep 1963, *J. Zaninovich* (CAS); vernal pool natural area in Valley Grassland, about 4.5 miles east-northeast of Pixley, 21 Sep 1967, *J. T. Howell* and *G. H. True 44006* (CAS); 4 mi N of Earlimart, 8 Aug 1971, *J. Zaninovich* (CAS); 3 mi E of Earlimart, 11 Jul 1975, *J. Zaninovich* (CAS); Earlimart, 28 Aug 1989, *H. C. Stutz 95143* (BRY); 2 mi W of Earlimart, 27 Apr 1992, *H. C. Stutz 95622* (BRY); 1 mi W of Earlimart, 2 Sep 1993, *H. C. Stutz 95921* (BRY); 3 mi W of Earlimart, 28 Aug 1994, *H. C. Stutz 9647* (BRY); 5 mi W of Earlimart, 5 Aug 1995, *H. C. Stutz 9787* (BRY); 3 mi S of Pixley on Airport Road, 5 Oct 1995, *H. C. Stutz 9841* (BRY).

Taxonomic relationships. *Atriplex subtilis* appears to be most closely related to *A. depressa* Jepson. They are both small-statured, somewhat obscure annuals with fine-textured stems, opposite branching and opposite sessile, cordate leaves. They differ in the shape of their fruiting bracts (deltoid in *A. subtilis*, rhomboid in *A. depressa*), position of fruiting bract appendages (on both surfaces of the fruiting bracts in *A. subtilis*, on adaxial side only in *A. depressa*), stem diameter (0.5–1.5 mm in *A. subtilis*, 1.0–2.0 mm in *A. depressa*), and internode length (20–30 mm in *A. subtilis*, 10–20 mm in *A. depressa*). They both often show red-purple stem pigmentation, but it is more common and more intense in *A. subtilis*.

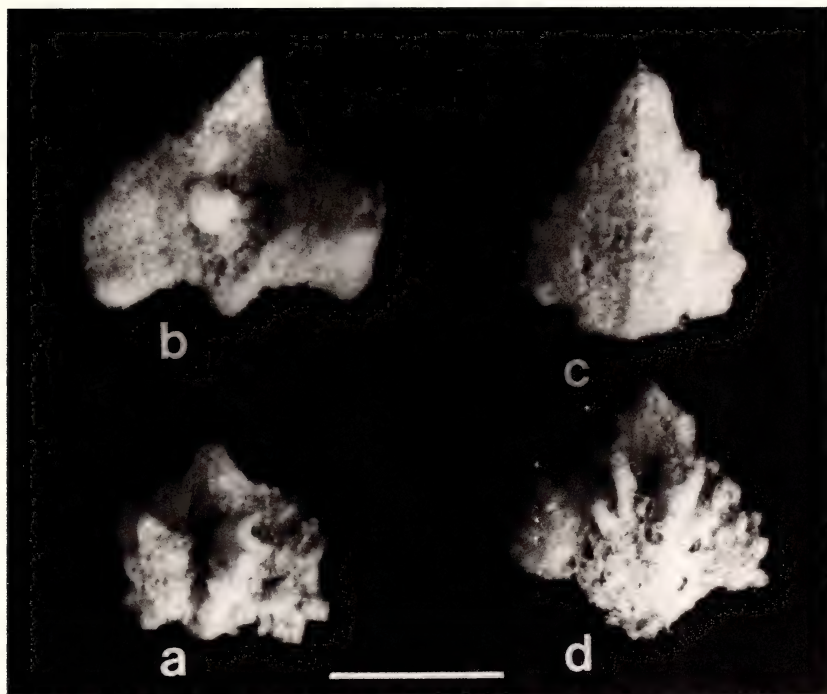


FIG. 2. Fruiting bracts of *Atriplex subtilis* and its near relatives. a. *Atriplex subtilis*. b. *Atriplex miniscula*. c. *Atriplex parishii*, d. *Atriplex depressa*. Bar = 2 mm.

than in *A. depressa*. *A. subtilis* occurs mostly in Fresno, Kern, Kings, and Tulare counties, California; *A. depressa* is restricted to more northerly latitudes, primarily in Glenn and Yolo counties.

Other near relatives of *A. subtilis* appear to be *A. parishii* Watson and *A. miniscula* Standley. Standley (1916) and Hall and Clements (1923) describe *A. parishii* as having alternate leaves. However the type (isotype) specimen (*S. B. and W. F. Parish 1119*, CAS), and plants collected in the field, 2 miles SE of Hemet, Riverside County, California, (*Stutz 9693*, BRY, and *9773*, BRY), and plants grown in the nursery at Brigham Young University, Provo, Utah (*Chu 9851*, BRY) from seed collected from plants in the Hemet population, all show mostly opposite leaves. As with *A. subtilis*, some of the upper branches of *A. parishii* plants have occasional alternate leaves but the lower leaves and branches are always opposite. *Atriplex miniscula* plants always have alternate branching.

Atriplex parishii is also distinguished from *A. subtilis*, *A. miniscula*, and *A. depressa* by its prostrate growth habit and pilose stems and fruiting bracts.

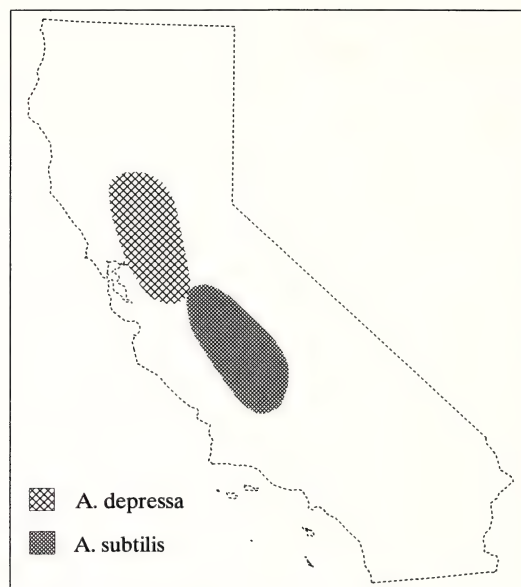


FIG. 3. Geographic distribution of *Atriplex subtilis* and *Atriplex depressa*.

KEY FOR *ATRIPLEX SUBTILIS* and its Near Relatives

1. Branches and leaves all alternate. *A. minuscula*
- 1'. Branches and leaves mostly opposite.
2. Stems prostrate; fruiting bracts unappendaged, pilose. *A. parishii*
- 2'. Stems erect; fruiting bracts with appendages, not pilose.
3. Leaves 2–4 mm long; each side of fruiting-bracts with 2 longitudinal rows of tuberculate appendages, fruiting-bracts near truncate at base. *A. subtilis*
- 3'. Leaves 3–7 mm long; fruiting-bract appendages not in rows, on abaxial surface only, fruiting-bracts near cuneate at base. *A. depressa*

ACKNOWLEDGEMENTS

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A NOMENCLATURAL NOTE ON *HASTINGSIA BRACTEOSA*
AND *HASTINGSIA ATROPURPUREA* (LILIACEAE)

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ABSTRACT

Populations of *Hastingsia bracteosa* s.l., including *H. atropurpurea*, were examined for macro-morphological differences, pollen size, viability and surface features, isozyme markers, phenology and color constancy in flowers and capsules. No discontinuity in morphological characters was found. Sympatric, intermediate and interfertile plants suggest the two taxa are too close to maintain as full species, and we propose reducing *H. atropurpurea* to a variety of the earlier name *H. bracteosa*.

In the Illinois River valley of Josephine Co., Oregon, an endemic lily is restricted to serpentine wetlands over a narrow 20 km long zone from Eight Dollar Mt. south to Woodcock Mt. It was described by Sereno Watson in 1885 as *Hastingsia bracteosa* (Proc. Am. Acad. 20:377, 1885) from white-flowered material collected at Eight Dollar Mt. After 1922 it was known as *Schoenolirion bracteosum* (S. Watson) Jepson (Fl. California 1:268, 1922). Peck (1962) noted its flowers were "dull white or purplish," but did not nomenclaturally segregate the species by flower color. Sherman and Becking (1991) argued to maintain the western members of the genus *Schoenolirion* in *Hastingsia*, as is generally done now (Smith & Sawyer 1988; McNeal 1993; Kartesz 1994a,b).

Some related genera (e.g., *Schoenolirion*, *Chlorogalum*) have species easily separable by perianth color (Becking 1986; Sherman 1969), but these taxa are also distinguished by clear morphological differences (e.g., presence or absence of a bulb, inflorescence branching, relative length of inflorescence and leaves).

Becking (1986) split *Hastingsia atropurpurea* Becking from *H. bracteosa* S. Watson based on (1) purple vs. white perianth, (2) largely allopatric ranges, (3) no evidence of hybrids or intermediates, and (4) morphological characters using the dimensions or density of bulb, scape, leaves, glaucousness, leaf venation, floral bracts, inflorescence bracts, raceme branching, and floral density in the racemes.

We found Becking's (1986) morphological data unconvincing and

were unable to validate the reported differences when we measured purple- and white-flowered plants randomly selected in the field (Lang et al. 1994 unpubl. report). Sherman & Becking (1991) used capsule color to discriminate the two taxa of *Hastingsia*, but we found this character did not correlate with flower color, and was variable to some degree with the maturity of the capsule.

Becking (1986, Fig. 2) mapped purple-flowered populations in wetlands south of Tennessee Mt. and white-flowered populations to the north. He noted only a few individuals that violated this pattern, and no populations of intermediates. This geographical segregation of floral color morphs is not as absolute as Becking maintained.

We sampled a north-south transect on the west side of the Illinois River valley, below Tennessee Mt. and Woodcock Mt. We found a gradual or clinal shift in the density of purple corolla pigment over 8 km. In the middle of the range, Zika (1987, unpublished report) discovered a mix of flower color morphs in a fen unknown to Becking at the time of his surveys (Becking 1982, Becking et al. 1982, unpublished reports). This fen supports hundreds of plants with flower colors of all possible extremes and intermediate colors, from purple to pink to white, growing side by side in the same microsites. We observed synchronous flowering and fruiting of all the individuals in this population, with pollinating bees visiting individuals regardless of their corolla color. Pollen viability was high in intermediate plants, as measured by staining with lacto-phenol cotton blue (Lang et al. 1994).

Further studies of surface pollen morphology across the range of both taxa, using SEM photography, showed as much variation within as between populations, and no discernable differences between taxa (Lang et al. 1994). Seed set was uniformly high regardless of flower color, even in the intermediate plants in the zone of sympatry (Lang et al. 1994). Isozyme analysis of ten loci from nine populations (Lang et al. 1994) showed no fixed allelic differences between the two taxa. In short, there was no apparent barrier to gene exchange between individuals with different flower colors.

Nonetheless a strong geographical component correlates with the perianth color extremes. The transition between the two color morphs is in a narrow zone of sympatry despite similar elevation, geology, hydrology, plant community, and other habitat preferences across the combined ranges of the two taxa. For these reasons we believe it is unwarranted to synonymize the two floral color morphs. On the other hand, a strong argument can be made to reduce the rank of *Hastingsia atropurpurea*. Species level morphological differences between the two taxa are essentially absent. All morphometric criteria used by Becking (1986) yield widely overlapping measurements (Lang et al. 1994). Furthermore, large numbers of interfertile and intermediate plants are found where the taxa are

sympatric. We have seen the following Josephine County, OR, specimens which we consider intermediate between *Hastingsia atropurpurea* and *H. bracteosa*:

Darlingtonia fen, 4 km SE of Tennessee Mt., elev. 455 m, T39S R8W S17 SW $\frac{1}{4}$, Zika 10397 OSC, 14 June 1987; same site, F. Lang 1794 OSC, 21 June 1993; Josephine Cr. ca. 3 km S of Tennessee Pass, elev. 510 m, T39S R9W S13 SE $\frac{1}{4}$ of SW $\frac{1}{4}$, J. Greenleaf 1094 OSC, 17 July 1981; *Darlingtonia* fen, E of Woodcock Mt., elev. 535 m, T39S R8W S19 SE $\frac{1}{4}$ of SE $\frac{1}{4}$, B. Mumblo s.n. OSC, 18 July 1984; creek in Westside Valley drainage, [a tributary to] Illinois River, elev. 535 m, T39S R8W S18 NW $\frac{1}{4}$ of SE $\frac{1}{4}$, B. Mumblo s.n. OSC, 18 July 1984; southern Josephine Co., L. Leach s.n. WILLU, 25 June 1930.

Based on the criteria used in Stuessy (1990), we propose reducing the rank of *H. atropurpurea* to a variety rather than a subspecies.

***Hastingsia bracteosa* (S. Wats.) var. *atropurpurea* (Becking) F. Lang & P. Zika, stat. et comb. nov.**—Basionym: *Hastingsia atropurpurea* Becking, Madroño 33:175.—TYPE: USA, Oregon, Josephine Co., O'Brien, Woodcock Mt., *Darlingtonia* bog, elev. 1520 ft., 4 July 1984, R. Becking 840700 (holotype, CAS!; isotypes, CAS, DS, GH, HSC, ORE, OSC!, PUA, RSA, SOC!, UBC, US).

Hastingsia bracteosa var. *bracteosa* was formerly a C1 candidate for listing as a federal Endangered Species (1980 Federal Register 45(242): 82480–82569), and faces threats across its limited range from mining, water theft, off-road vehicle use, grazing and development. Based on our investigations, we urge the U. S. Fish & Wildlife Service to place *H. bracteosa* var. *bracteosa* on its Species of Concern list, as it has already done for var. *atropurpurea*. Both varieties are narrow endemics and face the same threats in their limited aggregated habitat.

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A NEW VARIETY OF *AZORELLA DIVERSIFOLIA*
(APIACEAE) FROM SOUTHERN CHILE

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ABSTRACT

Azorella diversifolia var. **antillanca** is described as a new variety from Chile. This variety differs from *A. diversifolia* Clos ex Gay var. *diversifolia* by its divided leaves and a distribution primarily within the eastern portion of Region XI (Los Lagos).

RESUMEN

Se describe una nueva variedad, *Azorella diversifolia* var. *antillanca*, del Parque Nacional Puyehue, Chile. Esta variedad es diferente de *A. diversifolia* Clos ex Gay var. *diversifolia* en la división de sus hojas y una distribución en el este de Region XI (Los Lagos).

As part of her treatment of *Azorella* Lam. within Argentina, Martínez (1989) combined *Azorella incisa* (Griseb.) Wedd. with *Azorella diversifolia* Clos ex Gay. Originally these two species were distinguished by their degree of blade division and leaf-lobe composition (Clos 1847; Weddell 1857). Martínez (1989) found these characters to be too variable for the recognition of separate species. During a revision of *Mulinum* Pers. (Zech 1992), *A. diversifolia* has been further studied based upon field and herbarium collections. This additional examination showed consistent infraspecific variation supported by distribution and leaf morphology. Following Martínez (1989), and Stuessy's (1990) criteria for distinguishing infraspecific taxa, I therefore further refine the species and describe the following variety of *A. diversifolia*.

***Azorella diversifolia* var. *antillanca* Zech, var. nov.**—TYPE: CHILE, Región De Los Lagos, Prov. Osorno, Parque Nacional Puyehue, Antillanca Ski Resort on Volcán Blanca, at the curve in the road below the ski lift, 1990 m, 19 January 1990, *J. Zech et al.* 48 (holotype, OS: isotypes, CONC, GH, LB, UC).

Azorella diversifolia var. *antillanca* foliis incisis, plus trilobis sinubus 4.0–11.0 (6.1) mm; margine basi contiguo vel imbricato valde angusto vel clauso, foliis interdum variegatis.

Plants caespitose, 4–10 cm in diameter, herbaceous perennial. Rhizomes stout, 2–5 mm in diameter, branched, woody, distal portion with persistent leaf sheaths. Leaves basal, whorled, 3–6 cm long; blade rhomboidal to ovate, 10–24 mm long, 7–20 mm wide,

glabrous, variegated, bright yellow and green, or blade green, 3–5-lobed, sinuses 4.0–11.0 (6.1) mm deep, sinuses narrow with sides overlapping, lobes dentate; venation palmate; petiole 1.5–5.5 cm long, 1–3 mm wide at middle, leaf base clasping, margin pubescent. Umbels 2–6, 10–30 flowers per umbel; peduncle 0.5–4.5 cm long; involucre bracts 10–15, lanceolate, 6–8 mm long, glabrous or with marginal hairs. Flowers 5-merous, 2 mm in diameter, actinomorphic; calyx tubular with 5 distal lobes, green; corolla free, petals yellow, oblong, 1–2 mm long; stamens exserted, anthers red; pedicels 1–5 mm long. Fruit ovate to oblong, compressed dorsally, green, 2–4 mm long, 2 mm wide.

Azorella diversifolia var. *antillanca* differs from *A. diversifolia* var. *diversifolia* based upon characters of the leaves and distribution. Variety *antillanca*'s leaves are deeply lobed, the sinuses 4.0–11.0 mm deep with a mean of 6.1 mm, and may or may not be variegated, while var. *diversifolia*'s leaves lack variegation and the lobes may be shallow, the sinuses 1.75–3.5 mm deep with a mean of 2.7 mm, or absent. While some leaves of individual plants do display a mixture of blade morphology, the majority of leaves within a single plant are clearly of one or the other blade type described above. Leaf variegation was found within a single population of var. *antillanca* (J. Zech *et al.* 48; OS, CONC, GH, LP, UC) and may represent a further form of this variety.

Although *A. diversifolia* occurs within both Chile and Argentina, its primary distribution lies within Chile. Martínez (1989) reported only two collections for Argentina, within Provincias Santa Cruz (C. Hicken *s.n.*; SI) and Neuquén (P. Moreau *s.n.*; BA, UC!). The Neuquén material is var. *diversifolia* while the Santa Cruz material was not available for study. Within Chile, *A. diversifolia* occurs within Regions X and XI, in La Araucanía and Los Lagos, respectively. Variety *diversifolia* is found primarily in the north-west within Provincia Malleco with a concentration in and around Parque Nacional de Nahuelbuta (Fig. 1). Variety *antillanca* occurs primarily in the east within Provincias Osorno and Llanquihue (Fig. 1). Variety *antillanca* is found on and around Volcáns Osorno and Casa Blanca. While distinct distributions are present for both varieties, some overlap does exist (Fig. 1). The lack of mutual exclusivity may indicate that the species is undergoing initial divergence. Variety *antillanca* was named after the Refugio Antillanca above which the type specimen was collected.

The character of red anthers was not included in the original descriptions of Clos (1847) or Weddell (1857) or more recently by either Muñoz (1980) or Martínez (1989). Examination of further material has shown this character to be common to *A. diversifolia*

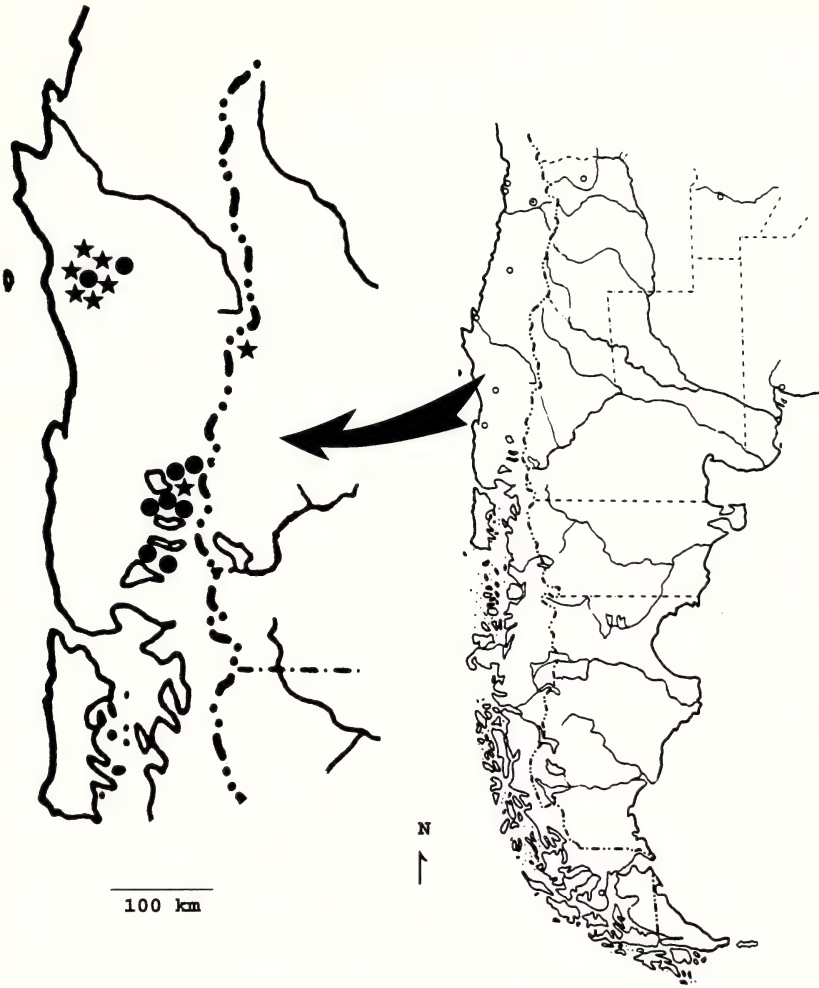


FIG. 1. Distribution of *Azorella diversifolia* var. *antillanca* and var. *diversifolia* within Chile and Argentina. Variety *antillanca* is indicated by solid circles and variety *diversifolia* by stars.

and a distinguishing feature in comparison to other species of *Azorella*.

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NOTES

REDISCOVERY OF *HEMIZONIA MOHAVENSIS* (ASTERACEAE) AND ADDITION OF TWO NEW LOCALITIES.—Andrew C. Sanders, Herbarium, Dept. of Botany and Plant Sciences, University of California, Riverside, CA 92521, and Darin L. Banks and Steve Boyd, Herbarium, Rancho Santa Ana Botanic Garden, 1500 N. College Ave., Claremont, CA 91711.

Hemizonia mohavensis Keck is a rare plant endemic to southern California, historically known from three collections made between 1924 and 1933, but not reported since. It has been widely thought extinct (e.g., Skinner & Pavlik, C.N.P.S. Inventory of Rare and Endangered Vascular Plants of California, 5th ed., 1994; Keil in Hickman, ed., The Jepson Manual: Higher Plants of California, University of California Press, 1993). The type locality is the Mojave River near Deep Creek (Keck, Madroño 3:4–18, 1935) at the north foot of the San Bernardino Mountains, San Bernardino County, but repeated searches in that area over the past 20 years have failed to find the plant. The locality reported for the earliest collection, San Jacinto Mountains in Riverside County, has been questioned (Skinner & Pavlik 1994) because the habitat cited, “chaparral hillside”, was so different from the type locality and because the few searches conducted failed to find the species. The range of the species, “s SnBr”, given in *The Jepson Manual* (Hickman 1993) is incorrect; it is not known from the south side of the San Bernardino Mountains.

Rediscovery and Known Distribution. In January 1994, Sanders and associates rediscovered *Hemizonia mohavensis* along both Twin Pines Creek and Brown Creek on the north slope of the San Jacinto Mountains. These collections were compared to an isotype and to two other specimens housed at RSA to confirm identification. Later it was discovered that the UCR Herbarium held two post-1933 collections of *H. mohavensis* from the San Jacinto Mountains, both misidentified as *H. kelloggii* E. Greene, and that these were from locations other than Twin Pines and Brown creeks—Hwy 243 at Lawlor Lodge and near Poppet Flat. Subsequent searches in fall of 1994 revealed additional populations farther up Twin Pines Creek, but failed to rediscover the Lawlor Lodge and Poppet Flat populations. The total population in fall 1994 in the Twin Pines Creek drainage was estimated at ca. 6000 plants. A search in fall of 1995 by J. Hirshberg, employed by the U. S. Forest Service, revealed additional populations in the Poppet Flat area and another site in the Twin Pines Creek drainage.

In October 1995, Banks and Boyd discovered the species in the Palomar Mountains of northern San Diego County. A series of sizable populations was found in Cutca Valley and adjacent areas of the Long Creek drainage. The total meta-population here was conservatively estimated at 10,000 individuals in the fall of 1995, but could easily have been several times larger. Based on the habitat at the Palomar site (ancient erosional surface with relatively gentle relief, granitic substrate, and desert transition chaparral vegetation), we conducted surveys in comparable areas of the Anza Bench to the northeast. Within this region, we discovered a series of populations in the vicinity of Indian Flats and in Chihuahua Valley, north of Warner Springs, San Diego County. The species was not encountered in the nearby areas of Riverside County, such as Tule Valley and Anza Valley, however.

The distribution of *Hemizonia mohavensis* appears to be highly discontinuous. Although it may be locally common where it occurs, it is limited to only a few very restricted habitat patches. All known populations occur between 850 and 1600 m elevation, but with most between 915 and 1225 m. The Lawlor Lodge site (1600 m) is highly anomalous in that the area is densely wooded with pines and oaks and there are no moist openings. The specimen was collected on the roadside (G. Helmkamp,

personal communication), which is the only open habitat present, and it appears to have been a waif. The area was thoroughly searched in fall of 1994, and no sign of the species was found.

The San Bernardino Mountains population of *Hemizonia mohavensis* remains enigmatic. Extensive searching in the vicinity of the type locality in 1994 and 1995 failed to locate the species. We believe that the type plants were waifs washed from an unknown population in vernal wet areas above. The type locality has been modified by construction of the Mojave River Forks Dam and upstream the Mojave River is flooded by Silverwood Lake. Possibly *H. mohavensis* occupied the area now under the lake. Although there appears to be potential habitat on the Las Flores Ranch, that area is private property and access has not been available. Many other areas in the San Bernardino Mountains have now been searched that do not appear to support the species. Areas surveyed in 1994 and 1995 that do not appear to support the species include Miller Cyn., West Fork Mojave River southwest of Silverwood Lake, margins of Silverwood Lake, Deep Creek from the Mojave River Forks Dam to Devil's Hole, Grass Valley at the crossing of Hwy 173 and upstream at the Pacific Crest Tr. (PCT), upper Horsethief Creek near the PCT, Horsethief Creek at Hwy 173, below the Mojave River Forks Dam on the Mojave River, Mojave River at the road crossing just southwest of Mojave River Forks Dam, Hwy 173 in the Las Flores Ranch area, Pilot Rock Ridge, and Hwy 173 from Mojave River Forks to Lake Arrowhead, notably along Kinley Creek.

Habitat preferences and biology. *Hemizonia mohavensis* occurs on gentle slopes and low gradient stretches of streams in otherwise mountainous terrain. It is generally found in grassy swales, at seeps, and along intermittent creeks in clay, silty, or gravelly soils which are saturated early in the year. Occasional plants may be found in drier sites near occupied wet areas, but these are always dwarfed. Surrounding slopes generally support xeric chaparral characterized by *Adenostoma fasciculatum* Hook. & Arn., *A. sparsifolium* Torrey, *Ceanothus greggii* A. Gray ssp. *perplexans* (Trel.) Jepson, and *Arctostaphylos glauca* Lindley. Streamside benches and open valley floors often support sizable stands of *Quercus agrifolia* Nee.

Hemizonia mohavensis seems to prefer areas where water accumulates and is available at depth through the summer. In this regard, the micro-habitat seems similar to that of other rare southern California *Hemizonia* species such as *H. arida* Keck and *H. floribunda* A. Gray, which also inhabit low moist areas, and rather dissimilar to that of such common species as *H. kelloggii* and *H. fasciculata* (DC.) Torrey & A. Gray, which inhabit dry fields, grasslands, and open slopes.

Flowering begins in July and continues through the fall and sometimes into winter if cold weather does not kill the plants. For example, when the initial rediscovery was made (1 January 1994), most plants were in fruit, and many were clearly decadent. Nevertheless, there were a fair number of individuals that still possessed a few open flowers, and a very few still heavily in flower.

The most recent floras covering southern California (e.g., Munz, A Flora of Southern California, University of California Press, 1974; Hickman 1993) state that the disk flowers of *H. mohavensis* are staminate and produce no fertile achenes. In fact, fertile disk achenes are present in most capitula, but may not be apparent in immature specimens. This discrepancy doesn't affect identification using the key in Hickman (1993), but might result in errors using Munz (1974).

Also, despite statements in the manuals (Hickman 1993; Munz 1974; Abrams & Ferris, An Illustrated Flora of the Pacific States, Stanford University Press, 1960) that *H. mohavensis* is 1.5 to 3 dm tall, it commonly reaches 1 m and sometimes 1.5 m. Plants under 3 dm are not uncommon, especially on habitat margins, but in good conditions the species will normally be taller. It appears the original collections were of relatively depauperate plants from marginal habitat or under drought conditions.

Conclusions. *Hemizonia mohavensis* still appears to be globally rare, but relatively stable, especially within the Cleveland National Forest. The currently known distribution (Fig. 1) suggests it is principally a Peninsular Range species, rather than one

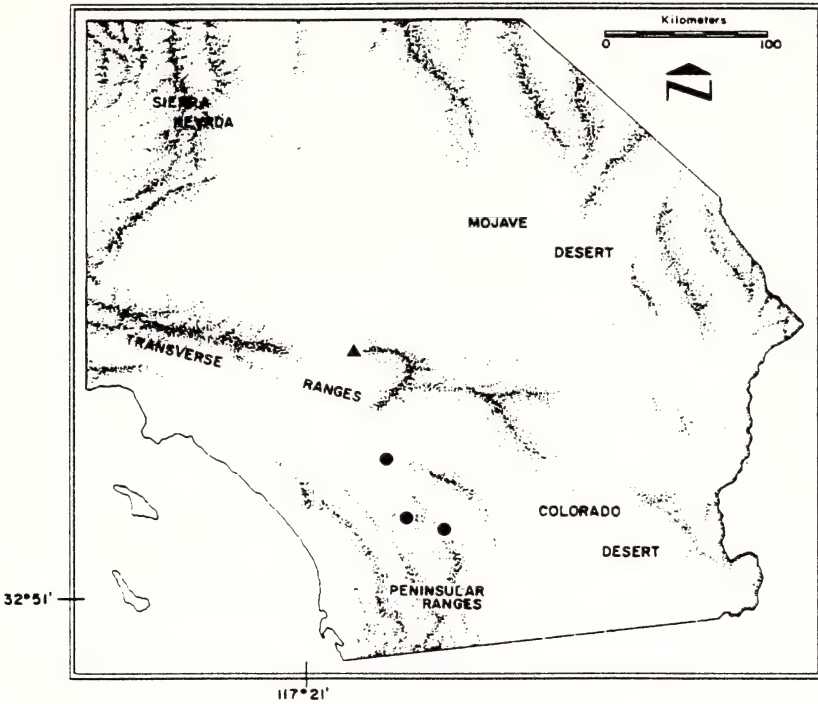


FIG. 1. Map of southern California showing approximate locations of known occurrences of *Hemizonia mohavensis*. Extant meta-populations are indicated by closed circles. The type locality (presumed extirpated) is indicated by a closed triangle.

of the Transverse Ranges or Mojave Desert margin as previously thought. With the better delimitation of habitat that we now have, it may be possible to find additional populations. Even within areas of generally suitable habitat, however, populations tend to be highly restricted, so very focused searches will be needed if additional sites are to be found.

Specimens examined. The following is a summary of all collections of *Hemizonia mohavensis* known to us.

California, Riverside County (all San Jacinto Mtns.): Banning-Idyllwild Rd., 3100 ft, 29 July 1924, *P. A. Munz & I. M. Johnston* 8880 (POM); Hwy 243, 1.6 km SE of Poppet Flat Rd, 4500 ft, 2 Oct 1977, *W. W. Mayhew s.n.* (UCR); Hwy 243 near Lawlor Lodge, 3.3 km N of Pine Cove, yellow pine and oak forest, 1600 m, 7 Oct 1989, *G. K. Helmkamp s.n.* (UCR); Brown Cr., Twin Pines Cr. drainage, 116°47'W, 33°53'N, T3S R2E S/2 NE/4 S29, hillside seep, 3120 ft, 1 Jan 1994, *A. C. Sanders* 14224 (RSA, UC, UCR); Brown Cr., 0.5 km above Twin Pines Cr., 116°47.5'W, 33°53'N, T3S R2E NE/4 S29, sandy bed of creek, 2920 ft, 4 Oct 1994, *A. C. Sanders, T. Schram & D. Wappler* 15771 (UCR); Twin Pines Cr. near Brown Cr., 116°48'W, 33°53'N, T3S R2E NW/4 S29, 856 m, sand along dry creek, 4 Oct 1994, *A. C. Sanders, T. Schram & D. Wappler* 15769 (UCR); 1.6 km SE of Twin Pines Ranch along draws between Pine Cr. and Dutch Cr., 116°47'W, 33°51.5'N, T4S R2E NW/4 NE/4 S4, formerly wet, grassy openings in chaparral, 1198 m, 6 Oct 1994, *A. C. Sanders, T. Schram & D. Wappler* 15793 (UCR); gorge of Azalea Cr., Twin Pines Cr. drainage, 116°48'W, 33°51.5'N, T4S R2E NW/4 NW/4 S5, low mead-

owy bench on creek bottom, 6 Oct 1994, A. C. Sanders, T. Schram & D. Wappler 15783 (UCR); Azalea Cr. and tributary gully from west, 116°48'W, 33°52'N, T3S R2E SW/4 SW/4 S32, formerly wet soil, 6 Oct 1994, A. C. Sanders, T. Schram & D. Wappler 15780 (UCR); Azalea Cr. 1 km SW of Twin Pines Ranch buildings, road crossing just outside fence, 116°48'W, 33°52'N, T3S R2E NW/4 SE/4 S32, 1070 m, sand along creek, 4 Oct 1994, A. C. Sanders, T. Schram & D. Wappler 15774 (UCR); tributary of Azalea Cr. 1.6 km due S of Twin Pines Ranch, 116°47.5'W, 33°51'N, T4S R2E center NE/4 S5, 1130 m, 4 Oct 1994, A. C. Sanders, T. Schram & D. Wappler 15775 (UCR); Brown Cr., 0.5 km above Twin Pines Cr., 116°47.5'W, 33°53'N, T3S R2E NE/4 S29, 915 m, 4 Oct 1994, A. C. Sanders, T. Schram & D. Wappler 15772 (UCR); S of Twin Pines Rd just W of Twin Pines Ranch entrance, 116°48'W, 33°52'N, T3S R2E SE/4 NW/4 S32, wash on canyon bottom, 6 Oct 1994, A. C. Sanders, T. Schram & D. Wappler 15789 (UCR); Twin Pines Ranch Rd, drainage 1 km NW of Twin Pines Ranch, T3S R2E NW/4 S32, 1100 m, 13 Sep 1995, J. Hirshberg s.n. (UCR); seeps and drainages along road to Hungry Hollow from Hwy 243, 1.6 km E of Poppet Flat, T4S R1E NW/4 S1, 1225 m, 13 Sep 1995, J. Hirshberg s.n. (UCR). **San Bernardino County:** Mojave River just below confluence with Deep Cr., low sand bars in the river bed, not more than ten plants found, 17 Sept. 1933, D. D. Keck 2531 (Holotype: UC; Isotype: RSA!); Mojave River at Deep Creek, 3000 ft, dry sandy river bed, 18 July 1933, L. C. Wheeler 1961 (RSA). **San Diego County:** NW of Hot Spring Mtn., Chihuahua Valley, 0.3 km S of Chihuahua Valley Rd on 9S05, open mesic swale in chaparral, T9S R3E NW/4 SE/4 S17, 1270 m, 7 Dec 1995, D. L. Banks & A. Sanders 0858 (RSA); 4.2 km S of Chihuahua Valley Rd on 9S05, open mesic swale in chaparral, T9S R3E NE/4 SW/4 S21, 1200 m, 7 Dec 1995, D. L. Banks & A. Sanders 0859 (RSA); (the following all Cleveland Nat. Forest); NW Palomar Mtns., Agua Tibia Mtns., Cutca Tr., Cutca Valley, 1 km outside the Agua Tibia Wilderness, at Cutca Rd (8S08), T9S R1E SW/4 NE/4 S18, 33°23'45"N 116°55'15"W, 3460 ft, 27 Oct 1995, D. L. Banks & S. Boyd 0853 (RSA); Cutca Tr., E of Cutca V., 0.3 km from Aguanga Tr., first major drainage, T9S R1E NW/4 NE/4 S16, 33°23'33"N 116°52'27"W, 3480 ft, 2 Nov 1995, D. L. Banks, et al. 0854 (RSA); Cutca Tr., 1 km W of Aguanga Tr., T9S R1E SE/4 NW/4 S16, 33°24'41"N 116°52'40"W, 3480 ft, 2 Nov 1995, D. L. Banks, et al. 0855 (RSA); Cutca Tr., 1.3 km W of Aguanga Tr., T9S R1E SE/4 NW/4 S16, 33°23'37"N 116°53'41"W, 3520 ft, 2 Nov 1995, D. L. Banks, et al. 0857 (RSA); hills N of Warner Springs and S of Chihuahua Valley, W of Hot Springs Mtn., Indian Flats Rd (9S05), 8 km N of Highway 79, T9S R3E S/2 SE/4 S35, ca. 3900 ft, 18 Nov 1995, S. Boyd 8529 (RSA); Indian Flats Rd, stream crossing 9.1 km N of Hwy 79, T9S R3E center S35, 3820 ft, 18 Nov 1995, S. Boyd 8530 (RSA); Indian Flats Rd, entrance to Indian Flats campground, T9S R3E SE/4 SE/4 S21, 3640 ft, 18 Nov 1995, S. Boyd 8531 (RSA); Indian Flats Rd, 14 km N of Hwy 79, T9S R3E NE/4 NE/4 S34, 3850 ft, 18 Nov 1995, S. Boyd 8532 (RSA).

DITTRICHIA GRAVEOLENS (ASTERACEAE), NEW TO THE CALIFORNIA WEED FLORA.—Robert E. Preston, Jones & Stokes Associates, 2600 V Street, Suite 100, Sacramento, CA 95818.

In November of 1994, I came across a nondescript composite that resembled a weedy member of the Aster tribe, while I was conducting a biological survey of the Alviso Marina in San Jose. Upon inspecting the plants, I found them to be of an unfamiliar species and collected specimens for later determination. I could not key them out using *The Jepson Manual* (Keil in Hickman (ed.), *The Jepson Manual: Higher Plants of California*, 1993), and I was ultimately unable to key them out using other North American manuals. Turning to the international floras, I found the plants to key out readily to *Dittrichia graveolens* (L.) Greuter in the *Flora of New South*

Wales (Brown *in* Harden (ed.), *Flora of New South Wales*, Vol. 3, 1992) and less readily in the *Flora Europaea* (Tutin et al., *Flora Europaea*, Volume 4, *Plantaginaceae* to *Compositae*, 1976). I confirmed the identity by comparison with specimens from the Mediterranean region at the Jepson/UC herbaria at Berkeley.

I contacted G. Douglas Barbe at the California Department of Food and Agriculture to find out if *Dittrichia graveolens* had been reported previously from California. He recalled having been sent a specimen several years ago. The late H. Thomas Harvey, professor of biology at San Jose State University, collected the species in 1984 near Alviso during his research on salt marsh ecology. He deposited his undetermined specimens with the herbarium at San Jose State University. In 1988, the late Carl W. Sharsmith, professor emeritus of botany at San Jose State, tentatively identified the specimens as *D. graveolens* and sent a duplicate specimen to the Department of Food and Agriculture for confirmation. No further action was taken on the discovery.

In November, 1995, Gail Rankin, botanist with the Santa Clara Valley Water District, called me to help identify a weedy plant that has become established in the Coyote Creek Revegetation Project at the north end of the Santa Clara Valley. The plants had first been noticed on the site around two years previously and have since spread rapidly throughout the revegetation area. I identified the plants as *D. graveolens*, based on her description, and confirmed the determination during a visit to the project site. Following this site visit, I drove to a number of other sites in the vicinity and located several other *D. graveolens* populations. The following collections encompass the currently known distribution in California, as I have been able to determine in the field and from herbarium collections (Herbaria consulted: AHUC, CAS, DAV, DS, HSC, JEPS, POM, RSA, SBBG, SD, SJSU, UC).

CALIFORNIA. Santa Clara Co.: two miles north of Alviso railroad tracks at upper edges of tidal marsh, 01 November 1984, *H. T. Harvey s.n.* (SJSU); south end of San Francisco Bay, at Alviso Marina, on banks of levee between parking lot and marina basin, elev. 1.5 m, 121°58'39"W, 37°25'49"N, Milpitas USGS 7.5' Quadrangle, 14 November 1994, *R. E. Preston 690* (DAV, UC, NY); Coyote Creek Revegetation Project, east side of levee adjacent to old Milpitas sewage disposal plant, elev. 3 m, *R. E. Preston & L. Spar 899* (DAV); northern San Jose (Alviso), in vacant lots north of State Street and west of Spreckles Street, elev. 1 m, 121°58'03"W, 37°26'00"N, Milpitas USGS 7.5' Quadrangle, 24 November 1995, *R. E. Preston 900* (DAV); Sunnyvale, Baylands Park, north side of bike path along State Route 237, elev. 2 m, 121°59'38"W, 37°24'38"N, Milpitas USGS 7.5' Quadrangle, 24 November 1995, *R. E. Preston 901* (DAV).

Dittrichia is classified in subfamily Asteroideae, tribe Inuleae (Bremer, *Asteraceae*, *Cladistics and Classification*, 1994). The genus consists of two species native to the Mediterranean region and introduced to other regions with semi-arid to semi-humid climates (Bremer 1994). Both species have been introduced into the United States, but neither appears to have become established, previously. *Dittrichia graveolens* has been collected in New York and New Jersey, and *D. viscosa* was collected on ballast in Florida, Pennsylvania, and New Jersey during the late 1800's (Herbaria consulted: TEX, GH, US, MO, NY). Cronquist (*Vascular Flora of the Southeastern United States*, 1980) noted that the Florida occurrence of *D. viscosa* does not appear to have persisted.

Dittrichia graveolens is an erect annual with sessile, lanceolate to linear leaves. The stems are 2 to 6 dm tall, branching above to produce a pyramidal inflorescence with many small heads in dense terminal racemes. The achenes are 2 mm long, subcylindric, pubescent with simple and glandular hairs, and abruptly narrowed at the apex, with a pappus of barbed bristles fused at the base to create a distinctive cup-like structure. *Dittrichia graveolens* superficially resembles *Aster subulatus* var. *ligulatus* and *Conyza* species but differs in having pale yellow corollas with anthers attached at the base and being pubescent on the stems, leaves, and inflorescence with glandular hairs. These same characters serve to differentiate *Dittrichia* from *Senecio*, to which specimens key using *The Jepson Manual*. The glandular hairs store terpenes,

which gives the plant a strong characteristic odor and is the basis of the common names "stinkwort" (Australia) and "stink aster" (Europe).

Dittrichia graveolens is a ruderal species that grows best in disturbed areas relatively free from competition with other species (Le Floe'h et al. in di Castri et al. (eds.), Biological Invasions in Europe and the Mediterranean Basin, 1990). The species primarily occurs in semi-arid to semi-humid regions (400 to 800 mm annual precipitation) and can withstand drought, although it does not tolerate excessive moisture (Parsons, Noxious Weeds of Victoria, 1973; Le Floe'h et al. 1990). The seeds germinate in March or April, and flowering occurs from September to October or later, if the weather remains favorable (Brown, The Weeds, Poison Plants, and Naturalized Aliens of Victoria, 1909; Parsons 1973). The achenes are dispersed primarily by wind and water, but the barbed pappus bristles also promote dispersal by animals and machinery (Parsons 1973). The seeds can remain viable in the soil for up to three years (Brown 1908).

The discovery of *D. graveolens* in the south Bay Area adds to the expanding list of invasive alien plants in California (Rejmánek and Randall, Madroño 41:161–177, 1994). The species appears to have high potential to become a widespread weed in California. One of the best predictors of invasiveness is whether a species is known to be invasive elsewhere (Panetta, Plant Protection Quarterly 8:10–14, 1993). *Dittrichia graveolens*, which was first recorded in Australia in 1850, has spread throughout the southern half of the country (Parsons 1973). The species has also become one of the main invaders of overgrazed range land in north Africa (Le Floe'h et al. 1990). The species has become established as a weed in several other regions, including Iran and Pakistan (Oztürk 1980, cited in Wacquant in di Castri et al. 1990); northwestern India (Chopra et al., Poisonous plants of India, 2nd ed., 1965); southwestern Cape Province in South Africa (Schneider and Du Plessis, Journal of the South African Veterinary Association 51:159–161, 1980); and South America (Bremer 1994).

Other indicators of invasiveness are whether a species has a close relative with a history of weediness in similar habitats and whether the seeds are dispersed by wind, mammals, or machinery (Panetta 1993). In the Mediterranean Basin, *D. viscosa* is an even more widespread weed than *D. graveolens*, although *D. viscosa* does not appear to have spread as far outside of the Mediterranean region (Wacquant 1990). *Dittrichia graveolens* plants produce copious small seeds that, as noted above, are readily dispersed. The California highway system provides a convenient corridor along which the species can migrate. Two highways (Interstate 880 and State Route 237) border the infestation sites, and the main highway to the Central Valley (Interstate 680) is less than 3 km east of the Coyote Creek location.

In addition to its potential to become a serious agricultural pest, *D. graveolens* has a several characteristics that warrant classification by the California Department of Food and Agriculture as a noxious weed. *Dittrichia graveolens* has been shown to cause allergic contact dermatitis (Burry and Kloot, Contact Dermatitis 8:410–413, 1982). The plants produce sesquiterpene lactones (d'Alcontres et al., Gazzetta Chimica Italiana 103:239–246, 1973; Rustaiyan et al., Phytochemistry 26:2603–2606, 1987; Lanzetta et al., Phytochemistry 30:1121–1124, 1991), which have been shown for many other composites to be linked to allergic contact dermatitis in humans (Mitchell and Dupuis, British Journal of Dermatology 84:139–150, 1971). Little evidence exists that the plants are toxic, although oxalate poisoning has been reported to be associated with grazing *D. graveolens* (Lamp and Collet, A Field Guide to Weeds in Australia, 1979), and fishermen in southern Italy reportedly use the macerated leaves to stun fish (Lanzetta et al. 1991). Livestock deaths due to ingestion of *D. graveolens* have been linked to enteritis caused by the barbed pappus bristles puncturing the small intestine (Gardner and Bennetts, The Toxic Plants of Western Australia, 1956; Schneider and Du Plessis 1980).

I thank Doug Barbe, Bruce Baldwin, and John Strother for their assistance in confirming the identity of my specimens; the collection managers at the herbaria cited for searching for additional specimens from California; Gail Rankin and Linda Spar

of the Santa Clara Valley Water District for calling my attention the Coyote Creek population, taking me on a tour of their revegetation site, and providing a lead to some of the references cited; and an anonymous reviewer for helpful comments on the manuscript.

NOTEWORTHY COLLECTIONS

CALIFORNIA

EUPHORBIA DENDROIDES L. (EUPHORBIACEAE).—Los Angeles Co., Angeles National Forest, Big Santa Anita Canyon, alt. 1000 ft., 16 Apr 1988, *Adelina Munoz* 87 (UCR); foothills above Pasadena, side canyon of Eaton Wash along New York Drive, 0.5 km N of Sierra Madre Blvd., alt. 300 m, 20 Apr 1996, *D. Koutnik s.n.* (UCR, and to be distributed).

Previous knowledge. Native to the Mediterranean basin and cultivated in California as an ornamental. Previously reported escaping in Santa Barbara Co. (C. F. Smith, *A Flora of Santa Barbara Region, California*, Santa Barbara Mus. of Nat. Hist., 1976), with specimens taken there at least as early as 1950, but not reported by Munz (*A California Flora*, 1959; *A Flora of Southern California*, 1974) or Koutnik (*in* J. C. Hickman, ed., *The Jepson Manual*, 1993). Also previously reported as “a well-established stand” in the foothills of the San Gabriel Mtns. near Pasadena (J. R. Brown, *Cactus and Succulent Society of America Journal*, 34:51–52, 1962). This record, which has been generally overlooked, was not documented by specimens although good photographs were provided.

Significance. First specimens from naturalized plants in Los Angeles County. This note serves to further document the need for addition of this species to state and regional floras.

EUPHORBIA ESULA L. (EUPHORBIACEAE).—Los Angeles Co., Malibu, coastal sage scrub near Malibu Creek, ca. 1 km N of the Pacific Coast Highway, 8 Oct 1992, *Scott White* 878 (UCR).

Previous knowledge. Native of Europe, North Africa and western central Asia, widely introduced into North America, and previously reported from northern California, with all known infestations from north of San Francisco (G. D. Barbe, *Noxious Weeds of California*, Distribution Maps, CA Dept. of Food and Agr., 1990, unpub. report; Koutnik, *in* Hickman 1993).

Significance. First record for Los Angeles County and southern California. A noxious weed in need of eradication.

EUPHORBIA HIRTA L. (EUPHORBIACEAE).—Riverside Co., Palm Desert, weed in lawns along a commercial strip on Hwy 111 between Hwy 74 and Sage Lane, 33°44'N, 116°22'W, alt. 45 m, 8 Nov 1994, *A. C. Sanders* 15864 (UCR, and to be distributed); Palm Springs, weed in lawns at a shopping center at the SE corner of Racquet Club Dr. and Palm Canyon Dr., T4S R4E center S3, alt. 200 m, 17 Mar 1996, *A. C. Sanders & G. Helmkamp* 17979 (UCR, and to be distributed); Rancho Mirage, weed in lawn at edge of Mission Hills Country Club, intersection of Dinah Shore Dr. and Duval Dr., T4S R5E NW/4 S26, alt. 100 m, 17 Mar 1996, *A. C. Sanders & G. Helmkamp* 17992 (UCR, and to be distributed).

Previous knowledge. A widespread weed in tropical America, and throughout the tropics, also occurs in Arizona, Texas and Florida.

Significance. First records for California. This species appears to have become a fairly common lawn weed in the Coachella Valley, and might be expected to appear elsewhere in southern California. It should certainly be sought in the Imperial and Borrego Valleys, which are closer to the probable Mexican source area and hence most likely already have established infestations.

This species would be placed in the genus *Chamaesyce* by Koutnik (*in* Hickman 1993), but *Euphorbia* without *Chamaesyce* (and *Pedilanthus*) is paraphyletic, making *Chamaesyce* unacceptable at generic rank if classification is to be based on phylogeny. We retain the more conservative and familiar classification.

The plants reported key to *Chamaesyce ophthalmica* (Pers.) Burch [*Euphorbia o.* Pers.] in the treatment of Burch (Ann. Missouri Bot. Gard. 53: 90–99, 1966), but this taxon is very doubtfully a distinct species from *E. hirta* and has been reduced to a variety of that species (e.g., A. C. Allen & B. E. Irgang, Tribe Euphorbieae, *in* Fl. Ilustrada do Rio Grande do Sol., Fasc. XI, Bol. Inst. Cent. Biosciencias [Brasil], ser. Botanica 34 (4): 1–97, 1975). If treated as a variety of *E. hirta*, it is correctly called *E. h.* var. *procumbens* (DC.) N. E. Br., not *E. h.* var. *ophthalmica* (Pers.) Allen & Irgang. We are uncertain whether variety *procumbens* is worthy of recognition, but note that all our collections are unambiguously referable to it.

EUPHORBIA NUTANS Lag. (EUPHORBIACEAE).—Riverside Co., Palm Desert, weed in landscaping along Hwy 111 between Hwy 74 and Sage Lane, 33°44'N, 116°22'W, alt. 45 m, 8 Nov 1994, A. C. Sanders 15863 (UCR); North Palm Springs (Garnet), weed in landscaping at I-10 and Indian Ave, T3S R4E SE/4 S15, alt. 250 m, 17 Mar 1996, A. C. Sanders & G. Helmkamp 17976 (UCR, and to be distributed).

Previous knowledge. Introduced from the southeastern U.S., Texas, Mexico, or South America. Uncommon and scattered on the coastal slope of southern California and north to the Sacramento Valley.

Significance. First records from the Sonoran Desert region of California and for Riverside County for this uncommon weed. This plant is called *Chamaesyce nutans* (Lag.) Small by Koutnik (*in* Hickman 1993).

EUPHORBIA OBLONGATA Griseb. (EUPHORBIACEAE).—Alameda Co., Strawberry Canyon fire trail, E of U. C. Berkeley, Centennial Dr. and Grizzly Peak Blvd, alt. 1200 ft., locally abundant, 26 Jun 1988, B. Ertter 7648 (DAV, RSA); Amador Co., Red Corral Road, 0.15 km W of road to P.G. & E. Powerhouse #7, N Fork of Mokelumne River, T7N R13E S33, abundant on south-facing slope, alt. 2500 ft., 1 Jun 1970, T. C. Fuller 19674 (RSA); Calaveras Co., Jurs Road, 2.5 km east and south of Westpoint, Middle Fork of the Mokelumne River, T6N R13E S12, scattered patches along drainageway, alt. 3000 ft., 1 June 1970, T. C. Fuller 19675 (RSA); Contra Costa Co., Martinez, along Franklin Creek in John Muir National Historic Site, 23 Apr 1981, W. E. Davis s.n. (DAV, RSA); Hwy 4, 5 km west of Martinez, 30 Jul 1958, T. C. Fuller s.n. (DAV); Alhambra Valley, ca. 6.6 km W of Martinez, 25 Jun 1959, T. C. Fuller 2679 (RSA); near Jewel Lake, C. L. Tilden Regional Park, common but local, alt. 500–600 ft., 28 Apr. 1979, R. A. Norris 3885 (RSA); Marin Co., Ross, spontaneous along Lagunitas Road, 25 Apr 1974, J. T. Howell 50327 (DAV); Napa Co., Hwy 29 south of Calistoga, T8S R7W S1, 1 May 1972, R. Lawley s.n. (DAV); San Joaquin Co., N side of Hwy 4, 1 km W of Woodsbro Rd., 4 mi. W of Stockton, 29 Sep 1958, M. Switzenberg s.n. (RSA); Santa Clara Co., Palo Alto, Chaucer Ave. on San Mateo Co. line, abundant, 9 Jun 1966, R. Thorne & P. Raven 86565 (RSA); Sonoma Co., Hwy

116, 7 km south of El Verano, T5N R6W S25, 31 May 1985, *T. C. Fuller 20430* (DAV); Yolo Co., Davis, a weed in a vacant lot in town, locally well established, ca. 1980, *D. Koutnik s.n.* (DAV, but specimen not currently available).

Previous knowledge. Native to the Balkans and Turkey. First reported in California from Sacramento County (P. Munz, *Aliso* 7 (1): 66, 1969). It was later reported from at least 20 counties from San Luis Obispo to Shasta via dots on a range map (Barbe 1990), but that report was not widely distributed and has escaped general notice. Koutnik (1993) reported it from "GV" and "SnFrB", but the constraints of the Jepson format may disguise the extent of the infestation.

Significance. First specimen records for Alameda, Amador, Calaveras, Contra Costa, Marin, Napa, San Joaquin, Santa Clara, Sonoma, and Yolo counties. This species has been present in California for about 40 years and appears well established in much of the northern half of the state. Documentation for additional areas would be very desirable.

EUPHORBIA REVOLUTA Engelm. (EUPHORBIACEAE).—Riverside Co., Santa Rosa Mtns., Deep Canyon below Bighorn Overlook along Hwy 74, 3600 ft., 15 Oct 1976, *J. Zabriskie 944* (UCR); San Diego Co., Anza-Borrego Desert State Park, north slope of Whale Peak, 10 km north of Agua Caliente Springs, T13S R6E S13, 4600 ft., 2 Sep 1982, *A. C. Sanders & F. C. Vasek 2916* (UCR).

Previous knowledge. Eastern Mojave Desert of San Bernardino Co. in California and through Arizona, New Mexico, Colorado, western Texas, and south to Chihuahua, Mexico.

Significance. Not reported for the Peninsular Range or Riverside or San Diego counties in any of the major floras [Munz 1959, 1974; Koutnik (*in* Hickman 1993)], but the Riverside Co. occurrence was noted in a species list in an appendix by Zabriskie (Plants of Deep Canyon and the Central Coachella Valley, California, Philip L. Boyd Deep Canyon Research Center, 1979), but that report seems to have escaped wide notice. Not reported for San Diego Co. by Beauchamp (A Flora of San Diego County, California, Sweetwater River Press, 1986). A range extension of ca. 200 km SW from the eastern Mojave Desert. This plant is called *Chamaesyce revoluta* (Engelm.) Small by Koutnik (*in* Hickman 1993).

EUPHORBIA TERRACINA L. (EUPHORBIACEAE).—Los Angeles Co., El Segundo Dunes, W of Los Angeles Intl. Airport, 33°56'N, 118°26'W, 100 ft., 4 Dec 1987, *A. C. Sanders 7584* (RSA, UCR); same location, 18 May 1988, *A. C. Sanders 7832* (RSA, UCR); Santa Monica Mtns., Corral Canyon Road about 0.5 km N of Pacific Coast Highway, at crossing of Solstice Canyon, alt. 10 m, locally common on roadside and along stream, 14 Mar 1996, *D. Koutnik s.n.* (UCR, & to be distributed); Marina Del Rey, disturbed N-facing slope above Ballona Creek, locally common (100–200 plants) over an area of ca. 0.2 ha, 33°58'N, 118°26'W, alt. 100 ft., 18 Mar 1996, *Scott D. White 3836* (UCR, & to be distributed).

Previous knowledge. Native to the Mediterranean region, eastern Europe and the Arabian peninsula.

Significance. First records for California; apparently reported from the U.S. only by Kartesz (A Synonymized Flora of the United States, Canada and Greenland, Timber Press, 1994), but on what basis and from where are unknown to us. This species has been at the Solstice Canyon locality since at least 1987 and was common and well established at that time, suggesting it had been present for a number of years. The species also occurs at Malibu Creek State Park (Suzanne Goode, pers. com., 1996).

versity of California, Riverside, CA 92521; DARYL KOUTNIK, Los Angeles County Planning Department, 320 W. Temple St., Los Angeles, CA 90012.

SONORA

METASTELMA CALIFORNICUM Benth. (ASCLEPIADACEAE).—Perennial vine with white flowers on shrub in sparse coastal thornscrub, Las Bocas on the Gulf of California, ca. 60 km (by air) S of Navojoa, Municipio de Huatabampo, 26°35'30"N 109°20'30"W, near sea level, *Van Devender* 92-121, S. L. Friedman, S. A. Meyer (1 Feb 1992, ARIZ, ARK), det. M. E. Fishbein.

Previous knowledge. Punta Prieta to the Cape Region in Baja California.

Significance. First Sonoran record for a Baja California species.

LOBELIA ENDLICHII (F. Wimmer) Ayers (CAMPANULACEAE).—Solitary annual in soil in hollow tree near stream, flowers bluish, Arroyo Los Pílares, ca. 23 km E of Yécora, 26 km W of Maycoba on México 16, Municipio de Yécora, 28°22'N, 108°47'W, 1300 m, *Van Devender* 95-478, *Reina G.* (6 May 1996, ARIZ), det. S. L. Friedman.

Previous knowledge. East of continental divide in Sierra Madre Occidental in SW Chihuahua (T. J. Ayers, *Systematic Botany* 15:296–327, 1990).

Significance. First Sonoran record.

ACOURTIA DIERINGERI R. L. Cabrera (COMPOSITAE).—Solitary herbaceous perennial, Cañada la Ventana, SE of Yécora on México 16, Municipio de Yécora, 28°21'45"N, 108°54'W, 1600 m, *Van Devender* 95-851, *Reina G.* (7 Sep 1995, TEX); uncommon 1.0 m tall herbaceous perennial, Arroyo Hondo, 11.5 km E of El Kípor on México 16, Municipio de Yécora, 28°26'30"N, 108°32'30"W, 1460 m, *Van Devender* 96-592, *Reina G.*, *G. Ferguson*, *L. Coyote* (11 Sep 1996, ARIZ, TEX), det. B. L. Turner.

Previous knowledge. Known only from the type locality in western Chihuahua: 20 km N of Basaseachic-Yepáchic road, 2150 m, *Cabrera* 628, *Dieringer* (23 Aug 1988, ENCB, GH, MEXU, TEX; L. Cabrera R. Sida 13:419–421, 1989).

Significance. First Sonoran records.

CONYZA APURENSIS Kunth (COMPOSITAE).—Common annual on disturbed roadside, Yécora, Municipio de Yécora, 28°22'25"N, 108°55'30"W, 1540 m, *Van Devender* 95-723, *Reina G.*, *D. A. Yetman*, *M. E. Fishbein* (6 Sep 1995, ARIZ, TEX, UCR), det. B. L. Turner.

Previous knowledge. Throughout the American tropics from the West Indies and South America north to Oaxaca, Guerrero and Michoacán on the Pacific slopes of México.

Significance. First Sonoran record.

LEIBNITZIA OCCIMADRENSIS Nesom (COMPOSITAE).—Common herbaceous perennial in pine-oak forest, 5.2 km W of Yécora on México 16, Municipio de Yécora, 28°21'48"N 108°59'12"W, 1720 m, *Van Devender* 96–85, *Reina*, *S. L. Friedman*, *W. Trauba* (11 Mar 1996, ARIZ, MEXU, TEX, det. B. L. Turner); 2 km SW of La Lobera, Municipio de Alamos, 27°16.3'N 108°37.4'W, 1450 m, *P. S. Martin s.n.*, *D. A. Yetman* (15 Mar 1992, ARIZ, det. R. K. Van Devender); Barranca Huicochic, bet. Huicochic and Sagaribo, Municipio de Alamos, 27°19–19.5'N 108°39'W, 1300–1600 m, *P. S. Martin s.n.*, *G. Ferguson*, *V. W. Steinmann*, *D. A. Yetman* (16–18 Mar 1992, ARIZ, det. R. K. Van Devender); shallow canyon bottom in pine-oak woods

below Sagaribo, Municipio de Alamos, 27°20'N 108°39'W, 1600 m, *M. E. Fishbein* 153, *D. A. Yetman* (17 Mar 1992, ARIZ), det. R. K. Van Devender.

Previous knowledge. In the Sierra Madre Occidental in Chihuahua and Sinaloa (G. L. Nesom, *Brittonia* 35:126–139, 183).

Significance. First Sonoran records.

MELAMPODIUM SERICEUM Lag. (COMPOSITAE).—Abundant annual, Yécora, Municipio de Yécora, 28°22'25"N, 108°55'30"W, 1540 m, *Van Devender* 95–732, *Reina G.*, *D. A. Yetman*, *M. E. Fishbein* (6 Sep 1995, ARIZ, TEX, UCR), det. B. L. Turner.

Previous knowledge. Pine-oak forests from El Salvador and Guatemala north to Central México and Chihuahua (T. F. Steussy, *Rhodora* 74:1–219, 1972).

Significance. First Sonoran record.

SENECIO RIOMAYENSIS B. L. Turner (COMPOSITAE).—Very common annual on steep, loose rocky slope in pine-oak forest, Ciénega de Camilo, 8.0 km E of El Kípor on México 16, Municipio de Yécora, 28°26'N 108°34'W, 1500 m, *Van Devender* 96–102, *S. L. Friedman*, *Reina G.* 13 Mar 1996, ARIZ, ASU, MEXU, RSA, TEX, UCR, USON), det. B. L. Turner.

Previous knowledge. Known only from the type locality in the Sierra Madre of eastern Sonora: Canyon de López, W of Mesa de Abajo, *P. S. Martin s.n.*, *G. Ferguson*, *K. Moore* (B. L. Turner, *Phytologia* 74:382–384, 1993).

Significance. Second collection for species.

IPOMOEA MADRENSIS S. Watson (CONVOLVULACEAE).—Herbaceous perennial from tuber in pine-oak forest, summit of Mesa Del Campanero between Yécora and Bermúdez (Chihuahua), Municipio de Yécora, 28°20'N, 109°02'W, 2120 m, *R. M. Turner* 85–30, *P. S. Martin* (1 Aug 1985, ARIZ); solitary herbaceous perennial in oak woodland along Arroyo El Kípor from El Kípor E to Tierra Panda (Las Taunas), Cordón Las Taunas, Municipio de Yécora, 28°24'N, 108°33'30"W, 1720 m, *Van Devender* 95–961, *Reina G.* (10 Sep 1995, FAU), det. D. F. Austin; rare herbaceous perennial in pine-oak forest, 6.6 km W of Yécora on México 16, Municipio de Yécora, 28°21'42"N, 108°59'06"W, 1760 m, *Reina G.*, *Van Devender*, *Búrquez M.*, *G. Ferguson*, *L. Varela* (5 Sep 1996, ARIZ); common herbaceous vine from underground bulb in pine-oak forest, Mesa del Campanero, Arroyo Largo, upper tributary of Barranca El Salto, Municipio de Yécora, 28°21'18"N, 109°01'48"W, 2000 m, *Van Devender* 96–397, *Reina G.*, *Búrquez M.*, *J. T. Columbus*, *G. Ferguson*, *J. F. Wiens* (6 Sep 1996, ARIZ, MEXU, RSA).

Previous knowledge. Michoacán, México, Nayarit, Zacatecas, and Chihuahua.

Significance. First Sonoran records.

CYCLANTHERA MINIMA (S. Watson) D. Kearns & C. E. Jones (CUCURBITACEAE).—Occasional delicate vine on muddy bank in pine-oak forest, Mesa Del Campanero, Arroyo Largo, upper tributary of Barranca El Salto, Municipio de Yécora, 28°21'30"N, 109°02'W, 2075 m, *M. E. Fishbein* 2591, *S. McMahon*, *D. A. Yetman* (9 Sep 1995, ARIZ); solitary annual vine in oak woodland along Arroyo El Kípor from El Kípor E to Tierra Panda (Las Taunas), Cordón Las Taunas, Municipio de Yécora, 28°24'N, 108°33'30–35"W, 1720 m, *Van Devender* 95–962, *Reina G.* (10 Sep 1995, ARIZ, det. M. E. Fishbein); uncommon annual vine in shady canyon in pine-oak forest, Puerto de la Cruz, north base of Mesa del Campanero, Municipio de Yécora, 28°22'37"N, 109°02'W, 1900 m, *Reina G.* 96–490, *Van Devender*, *G. Ferguson*, *J. T. Columbus*, *J. T. Porter* (8 Sep 1996, ARIZ, MEXU, MO, NY, UCR).

Previous knowledge. Chihuahua, Sinaloa (D. M. Kearns and C. E. Jones, Madroño 39:301–303, 1992).

Significance. First Sonoran records.

RHYNCHOSPORA CONTRACTA (Nees) J. Raynal (CYPERACEAE).—Locally common annual in moist soil on open slope, Las Piedras Canyon, northeastern Sierra de Alamos, 3.2 km (by air) S of Alamos, tropical deciduous forest, Municipio de Alamos, 26°59'20"N, 108°56'45"W, 550 m, *Van Devender 95-1141, Reina G.*, (3 Oct 1995, ARIZ, MEXU, RSA), det. E. Roalson.

Previous knowledge. SE US; West Indies; from South America north to Veracruz and Nayarit, México; West Africa.

Significance. First Sonoran record.

BERNARDIA MYRICIFOLIA (Scheele) S. Watson (EUPHORBIACEAE).—Common 1.5–2.0 m shrubs on bare volcanic ledges top of canyon, Cruz del Diablo (Cañada Maimodochi), Cerro El Lobo, 7.5 km (by air), 13.2 km (by road) NE of Huasabas on road to El Coyote, Municipio de Huasabas, 29°56'18.2"N, 109°14'14.4"W, 1240 m, *Van Devender 95-535, Reina G., J. J. Sánchez E.* (27 May 1995, ARIZ, RSA, USON [Universidad de Sonora]), det. V. W. Steinmann.

Previous knowledge. From south central New Mexico and central and southern Texas south to Tamaulipas, Nuevo León, and Coahuila.

Significance. First Sonoran record. A southwestern range extension of ca. 350 km from Doña Ana Co., New Mexico.

EUPHORBIA NUTANS Lag. (EUPHORBIACEAE).—Common annual in field on hillside in oak woodland, along Arroyo El Kípor just E of El Kípor on trail to Tierra Panda (Las Taunas), Municipio de Yécora, 28°24'N, 108°33'35"W, 1740 m, *Van Devender 95-967, Reina G.* (10 Sep 1995, ARIZ, RSA, USON); common annual near stream, Arroyo El Otro Lado, Mesa El Otro Lado, 1 km NE of Yécora on old road to Maycoba, pine-oak forest, Municipio de Yécora, 28°23'10"N, 108°54'55"W, 1540 m, *Van Devender 95-815 & 95-873, Reina G., D. A. Yetman, M. E. Fishbein*, (7 Sep 1995, ARIZ, ARIZ, RSA, USON); common annual on roadside in pine-oak forest, 0.3 km W of Restaurant Puerto de la Cruz on México 16, north slope of Mesa del Campanero, Municipio de Yécora, 28°22'30"N 109°01'48"W, 1900 m, *Van Devender 96-544, Reina G., G. Ferguson, J. T. Columbus, J. M. Porter* (9 Sep 1996, ARIZ, MEXU, RSA, TEX, UCR), det. V. W. Steinmann.

Previous knowledge. Widespread in warmer parts of the world, in US from New York to South Dakota to central and western Texas.

Significance. First Sonoran records.

DIGITARIA TERNATA (A. Rich.) Stapf (GRAMINEAE).—Uncommon annual in moist soil, Arroyo El Otro Lado, Mesa El Otro Lado, 1 km NE of Yécora on old road to Maycoba, pine-oak forest, Municipio de Yécora, 28°23'10"N, 108°54'55"W, 1540 m, *Van Devender 95-835, Reina G., D. A. Yetman, M. E. Fishbein* (7 Sep 1995, ARIZ, USON), det. J. R. Reeder.

Previous knowledge. Aguascalientes, Guanajuato, Hidalgo, Jalisco, México, Michoacán, and Sonora (2.1 km NW of Matarichi, Municipio de Sahuaripa, *R. S. Felger 94-387B*, ARIZ).

Significance. Second Sonoran collections of an introduced African annual.

PASPALUM PALMERI Chase (GRAMINEAE).—Uncommon perennial, Agua Amarilla (Los Pinitos), 15 km WNW of Tepoca, 24.7 km WNW of San Nicolás on México

16, km 200 east of Hermosillo, red volcanic barren with isolated *Pinus yecorensis-Quercus albocincta* woodland, Municipio de Onavas, ca. 28°08'20"N, 109°20'23"W, ca. 900 m, *Van Devender 95-774, Reina G., D. A. Yetman, M. E. Fishbein*, (6 Sep 1995, ARIZ, RSA, USON), det. J. R. Reeder.

Previous Knowledge. Only known from the type collection. (*E. Palmer 704* in Sep 16–30, 1890, Alamos, Sonora, US; A. Chase, Contr. US Nat. Herb. 28:109, 1929).

Significance. Second collection of a little known grass. A northern range extension of 165 km. Its' relationship to the widespread *P. langei* (E. Fourn). Nash. warrants additional study.

DALEA TENTACULOIDES Gentry (LEGUMINOSAE).—Common 1.0 m tall shrub in shady understory in oak woodland in rocky canyon, Cruz del Diablo (Cañada Maimodochi), Cerro El Lobo, 7.5 km (by air), 13.2 km (by road) NE of Huasabas on road to El Coyote, Municipio de Huasabas, 29°56'18.2"N, 109°14'14.4"W, 1240 m, *Van Devender 95-532, Reina G., J. J. Sánchez E.* (27 May 1995, ARIZ, NY, USON), det. S. McMahon.

Previous knowledge. Southern Arizona. The species is an U. S. Fish and Wildlife Service Category 1 candidate.

Significance. First record for Sonora and México.

TRIFOLIUM AMABILE H.B.K. (LEGUMINOSAE).—Locally common herb near stream, Mesa El Otro Lado, 1 km NE of Yécora on old road to Maycoba, pine-oak forest, Municipio de Yécora, 28°23'10"N, 108°54'55"W, 1540 m, *Van Devender 95-814, Reina G., D. A. Yetman, M. E. Fishbein* (7 Sep 1995, ARIZ, MEXU, UCR, USON); uncommon herbaceous perennial in grassy area along street, Yécora, Municipio de Yécora, 28°22'25"N, 108°55'30"W, 1540 m, *Van Devender 95-733, Reina G., D. A. Yetman, M. E. Fishbein* (6 Sep 1995, ARIZ), det. P. D. Jenkins.

Previous knowledge. SE Arizona; widespread in Mexico from Chihuahua, Durango, and Sinaloa, south to Central America.

Significance. Although expected for Sonora, these are the first collections.

BOTRYCHIUM SCHAFFNERI Underw. (OPHIOGLOSACEAE).—Solitary fern in understory in riparian pine-oak forest in stream canyon, 3–4 km NNW of El Kípor, Municipio de Yécora, 28°25'30"N, 108°36'20"W, 1640 m, *Van Devender 95-390, Reina G.,* (4 May 1995, ARIZ), det. G. Yatskievych.

Previous knowledge. Widespread in México from Chihuahua southward to Central and South America; West Indies.

Significance. First Sonoran record.

CAMPYLONEURUM ANGUSTIFOLIUM (Sw.) Fee (POLYPODIACEAE).—Moist pine-oak woods, waterfall at Saguaribo, Municipio de Alamos, 27°20'N, 108°39.8'W, 1550 m, *P. S. Martin s. n., D. A. Yetman* (17 March 1992, ARIZ, det. G. Yatskievych, 1996), solitary, large clump on cliff face, Los Pílares, Arroyo Los Pílares, ca. 23 km E of Yécora, 26 km W of Maycoba on México 16, Municipio de Yécora, 28°23'N, 108°47'W, 1260 m, *Van Devender 95-902, Reina G., D. A. Yetman, M. E. Fishbein* (8 Sep 1995, ARIZ, MO, UCR, USON), ver. G. Yatskievich.

Previous knowledge. Florida in US; widespread in México from Chihuahua southward to Central and South America; West Indies.

Significance. First Sonoran records.

CRUSEA PARVIFLORA Hook. & Arn. (RUBIACEAE).—Locally common annual, Agua Amarilla (Los Pinitos), 15 km WNW of Tepoca, 24.7 km WNW of San Nicolás on

México 16 at km 200, red volcanic barren with isolated *Pinus yecorensis-Quercus albocincta* woodland, Municipio de Onavas, ca. 28°08'20"N, 109°20'23"W, ca. 900 m, *Van Devender 95-752A, Reina G., D. A. Yetman, M. E. Fishbein*, (6 Sep 1995, ARIZ, PTBG), det. D. H. Lorence.

Previous knowledge. Pacific slopes of México from Sinaloa and Durango south to Costa Rica (W. R. Anderson, Mem. New York Bot. Garden 22:1-128, 1972).

Significance. First Sonoran record.

NICANDRA PHYSALODES (L.) Gaertn. (SOLANACEAE).—Common 1.5 m tall coarse annual in corn field (said to be contaminant in seed purchased in Cd. Obregón), Los Pilares, Arroyo Los Pilares, ca. 23 km E of Yécora, 26 km W of Maycoba on México 16, Municipio de Yécora, 28°23'N, 108°47'W, 1260 m, *Van Devender 95-900, Reina G., D. A. Yetman, M. E. Fishbein* (8 Sep 1995, ARIZ, MEXU), det. P. D. Jenkins.

Previous knowledge. Monotypic genus native to Perú, established in many warmer areas, in US from Nova Scotia to Florida, a waif in California; México to Costa Rica; northern South America; West Indies.

Significance. First Sonoran record.

TRIUMFETTA CHIHUAHUENSIS Standl. (TILIACEAE).—Rare 1.9 m tall shrub, Los Pilares, Arroyo Los Pilares, ca. 23 km E of Yécora, 26 km W of Maycoba on México 16, Municipio de Yécora, 28°23'N, 108°47'W, 1260 m, *Van Devender 95-881, Reina G., D. A. Yetman, M. E. Fishbein* (8 Sep 1995, ARIZ, TEX); common 1.5-2.0 m tall shrub in sycamore-pine-oak forest canyon, El Aguajito, Barranca Honda, north slope of Mesa del Campanero, 4.8 km W of Puerto de la Cruz on México 16, Municipio de Yécora, 28°22'18"N, 109°02'54"W, 1640 m, *Van Devender 96-554, Reina G., G. Ferguson, J. M. Porter, J. T. Columbus* (8 Sep 1996, ARIZ, MEXU, NMC, RSA, TEX, UCR, USON); uncommon 1.2 m tall shrub, Arroyo Hondo, 11.5 km E of El Kípor on México 16, Municipio de Yécora, 28°26'30"N, 108°32'30"W, 1460 m, *Van Devender 96-605, Reina G., G. Ferguson, L. Coyote* (11 Sep 1996, ARIZ, MEXU, TEX), dets. P. A. Fryxell.

Previous knowledge. Described from Guayanopa Canyon, Sierra Madre Occidental, Chihuahua (P.C. Stanley 1923, Contr. US Nat. Herb. 23:744).

Significance. First Sonoran records.

—ANA LILIA REINA GUERRERO, Herbarium, University of Arizona, Tucson, AZ 85721; THOMAS R. VAN DEVENDER, Arizona-Sonora Desert Museum, 2021 N. Kinney Road, Tucson, AZ 85743; ALBERTO BURQUEZ MONTIJO, Centro de Ecología-UNAM, A. P. 1354, Hermosillo, Sonora 83000, México.

OBITUARY

MARION STILWELL CAVE
(1904–1995)

When Marion Cave passed away on 26 September 1995, at age 91, it marked the end of a remarkable life and a significant career in botanical research. In a period spanning nearly 40 years, Marion Cave made pathbreaking contributions to plant genetics, cytology, and embryology that went well beyond her modest status as a research associate in the Botany Department, University of California, Berkeley. Moreover she was such a significant influence on graduate students and foreign colleagues that it was a surprise to many that she did not hold a regular academic post. Not only did she provide an example of the highest standards of technique and critical thinking, but she also was a model of personal determination and integrity.

Marion was born in Rochester, New York, on February 11, 1904. Her family later moved to Denver, Colorado. Marion attended the University of Colorado, where she obtained an A.B. degree in Biology in 1924, election to Phi Beta Kappa, and an A.M. degree. She came to Berkeley as a graduate student and, in 1928, married Roy Clinton Cave. Roy earned a Ph.D. degree in Economics at Berkeley, and then made his career as a Professor of Economics at San Francisco State University. Marion obtained a Ph.D. in genetics in 1936, with a dissertation on the cytogenetics of *Crepis*, under the direction of Ernest Brown Babcock. This work demonstrated that the "generic" differences used to separate a species given generic status as *Rodigia* were due to slight genetic differences from the widespread *Crepis foetida*, a pioneering application of genetics to plant taxonomy.

From 1936 to 1943, Marion worked as a Research Associate in the Botany Department at Berkeley, launching a series of studies on sporogenesis and gametogenesis of various Liliaceae. She also carried out a series of collaborative studies with W. W. Wager on the cytology and cytogenetics of fungi, including members of the genera *Phytophthora*, *Cronartium*, and *Fomes*. It was during this period that she began her 20-year-long collaboration with Lincoln Constance on studies of chromosome numbers in the Hydrophyllaceae. At the time this series was initiated, this collaboration on Hydrophyllaceae represented one of the early applications of chromosome studies and numbers to phylogenetic deductions.

Marion and Roy spent 1944–45 in Washington, D.C., working for the U. S. Government in the Office of the Coordinator of Inter-American Affairs. During that time, she published a series of translations of Forest Legislation in a range of Central American, South American, and Caribbean countries.

Returning to Berkeley in 1945, Marion resumed her status as Research Associate in the Botany Department. Not only did she continue her collaborative work with Constance, but she initiated new associations with entirely different goals. For example, in the early 1950s Marion developed a research collaboration with Dr. Mary Pocock of Rhodes University in Grahamstown, South Africa. Pocock was one of the world's authorities on the systematics and morphology of the Volvocacean green algae. They collaborated in publishing one of the first studies on the karyology of algae. Not only did they develop new techniques to study this material, but they also were working in largely uncharted territory with regards to algal chromosome morphology and numbers. This was one of the earliest algal chromosome papers to have photographic documentation. Marion was awarded a Guggenheim Fellowship to support her visit to South Africa to carry out this collaboration.

During the 1950s, Marion had an altogether different type of research association with Spencer W. Brown of the Berkeley Genetics Department. From the mid- to late

1950s, they published elegant experiments on the role of pollen grain and stigma/ovule interactions in dominant lethals of *Lilium*. These studies established, for the first time, the existence of a "preferred zone" of ovules to which the pollen tubes were first attracted.

In this period and into the 1960s, Marion continued her studies of embryology in Liliaceae and became one of the foremost proponents of the use of embryological data in plant systematics. Not only did she produce significant publications on this subject, but she also organized a symposium for the Ninth International Botanical Congress in Montreal, Canada, in 1959.

One of the most fascinating studies Marion made was initiated because of an international controversy that had developed in the field of plant embryology. In 1957, Russian embryologists M. S. Yakovlev and M. D. Yoffe published an account of embryogenesis in species of the genus *Paeonia* (Paeoniaceae), in which they reported that early development of its proembryo was free-nuclear like that of gymnosperms. The Russians' article was published in the Indian Journal "Phytomorphology", founded and edited by the famous embryologist, Panchanan Maheshwari. Maheshwari did not believe the Russian report and had one of his own students, Dr. Prem Murgai, repeat the work. They came to an entirely different interpretation from the Russians.

Marion Cave became interested in this controversy. Together with two Berkeley graduate students, Howard Arnott (now at University of Texas, Arlington) and Stanton A. Cook (now at University of Oregon, Eugene), she published a much more extensive and critically documented 1961 paper that supported the Russians' interpretation. Marion had not expected to find that the Russians were correct, but faced with her own critical data and bedrock of scientific integrity, she could not interpret her results otherwise.

An interesting sidebar to this story is that Maheshwari visited Berkeley in the fall of 1963, to meet with Marion and convince her of the validity of the Indian interpretation. To this purpose he had brought slides from Dr. Murgai's study. One of us (DRK) had the pleasure of attending their meeting. Maheshwari was a large man, virtually twice the size of Marion, with an ebullient, dominating personality. It was clear that he was used to winning arguments based largely on the force of his personality. Thus, in that session, he attempted to overpower Marion. However, she would not have any of it. In her typical fashion, she quietly stuck to her guns and effectively pointed out where he and his student had made their mistake. She even had a young graduate student with some embryological experience look at his slides. It was clear, even to a novice, that Maheshwari and his student had misinterpreted their preparations. This episode illustrated both Marion Cave's strong resolve and the fact that she could never be cowed by any authority figure, no matter how famous.

Another example of Marion's strong will and personal resolve occurred after her 1970 monograph *Chromosomes of Californian Liliaceae* was reviewed by a member of the staff at Kew Gardens in the Kew Bulletin. The reviewer accused Marion of having inked in the images of chromosomes in her photographs because her preparations were so beautiful. Needless to say, Marion was madder than the proverbial "wet hen" and wasted no time in setting that reviewer straight!

One of Marion's lasting contributions to plant cytology and cytogenetics was the initiation of the "Index to Plant Chromosome Numbers", of which she was the initial Editor, from 1956–1964, and Associate Editor from 1964–1974. The index is an annual compilation of published chromosome numbers from the plant literature. It was organized with a group of compilers who scoured the literature in assigned journals, then sent in chromosome counts with the literature citation to the editor. Marion not only conceived the idea for this reference work, but also procured National Science Foundation grants to support its launching. It has proved to be an enduring and useful resource.

Beyond her own research and scholarly contributions, Marion contributed significantly to the education and training of graduate students at Berkeley. Former grad-

uates Howard Arnott, Sherwin Carlquist, Stan Cook, and Florence and Herb Wagner have written to indicate how central Marion was to their own research training. She not only taught them, and others, the essentials and finer points of plant microtechnique and photomicrography, but also how to interpret the more arcane aspects of plant embryology and chromosome structure.

Her personal generosity was not restricted to the Berkeley campus. An avid traveler world-wide, she developed close personal friendships on virtually every continent and would go out of her way to help wherever there was need. For example, in the post-World War II period, Marion sent slides, coverglasses, and other materials to Dr. Rosalie Wunderlich of the University of Vienna, so that Dr. Wunderlich could restart her embryology research program in war-torn Vienna.

Dr. Florence Wagner, who lived with the Caves for two years after World War II, characterized Marion as "a cheerful complainer and a happy pessimist, a person who was intensely aware of what was wrong with the world but who was a realist with a genuine sense of humor." Marion had an interest in all aspects of life and was an avid reader, gardener, and even designed and made all of her own stylish clothing, and (with Ray) their Berkeley Hills home. At the end of her Berkeley career, she became the Botany Department's resident photographer, making portraits of faculty and graduate students.

Since Marion was not a UC faculty member, she had to carry out her research in the modest space and facilities accorded graduate students. Despite this, she managed to carry out a remarkably diverse series of careful, original, and technically difficult studies. If Marion were beginning her scientific career today, she would have become a full-fledged faculty member in a noted academic institution such as Harvard or Berkeley. However, we doubt that she would have made any more impact. The fact that she accomplished so much without that status underscores her truly remarkable nature and the source of her lasting influence.

Volume 33 (1986) of *Madroño* was dedicated to Marion Cave.

—DONALD R. KAPLAN, LINCOLN CONSTANCE, and ROBERT ORNDUFF, University of California, Berkeley.

REVIEWS

A Manual of California Vegetation. By JOHN O. SAWYER and TODD KEELER-WOLF. 1995. California Native Plant Society, Sacramento, California. 471 pp.

This volume is arguably one of the most important ever to appear on the subject of California vegetation. It is significant because it is comprehensive—it attempts to classify and give a description of every known type of vegetation—and, perhaps even more because of its biopolitical implications—the authors are explicit that their aim is to make the manual the basis for setting vegetation-based priorities in the struggle to save California's diminishing natural ecosystems. It also carries special weight because it is the outgrowth of extended discussions of a large committee formed by the California Native Plant Society (CNPS) that included a broad spectrum of experts from universities, state and federal agencies, consulting firms, and private conservation organizations. It implicitly carries the imprimatur of the State of California because the second author is with the Department of Fish and Game, as were a number of committee members. A book with this lineage, this content, and these aspirations deserves careful review.

The nicely designed cover, with its striking photo, set a tone appropriate to the grandeur of the subject. This is further sustained by a collection of 32 plates with over 160 outstanding photos that may be the best comprehensive collection of color pictures illustrating California vegetation ever assembled in one book. Purchase of the book can almost be recommended solely on the basis this collection of photos.

The text consists of introductory and explanatory material (about 6% of the book), keys and descriptions of the individual vegetation types (series and others—about 73%), an extensive bibliography, an appendix describing the CNPS-approved sampling scheme, and indices of vegetation names, species, and a table that gives the equivalents between the Natural Diversity Data Base system developed by Robert Holland and the present system (hereafter Sawyer/Keeler-Wolf or SKW). The book is thus a “manual of vegetation” in the same sense that the keys and plant descriptions of a flora can be a “manual of the plants”.

The scheme by which the diverse vegetation of this very large state is classified is said by the authors to be hierarchical, but they do not provide an overall description of the hierarchy. The keys work only for the central unit of their system, the “series”. The series is not explicitly defined, but it is possible to deduce that it is a plant community that recurs at several to many sites with substantially the same species composition and structure and that is usually (but not always) characterized by the presence of one or a few defining species or genera that are usually (but not always) dominant. Rather surprisingly, no scale is specified for the series either as an individual stand occurrence or cumulatively for all stands, excepting the implicit requirement that a series be a repeating landscape unit. Thus, a single occurrence of a series in the landscape can be as small as a few meters across (duckweed series or quillwort series) or as large as many square kilometers (California annual grassland or creosote bush series).

The authors state clearly that their emphasis is on floristics and rarity. This leads to what some will surely consider a bias toward the vegetation equivalent of “splitting”. Thus by SKW, most saltmarshes, ecosystems that have literally been the poster-communities for integrated function, will include several series (pickleweed series, cordgrass series). The overriding importance of floristics is further illustrated by the fact that the pickleweed series is said to occur both in salt marshes and in inland salt flats—only generic dominance, not habitat or ecological relations—matters. To many

ecologists, this approach will seem to have taken apart things that should be left together and to have lumped things that should be clearly distinguished.

The names of most series are composed of the common name of the single dominant species or the collection of names of the two or three dominants. Others series are named for genera (Quillwort series), and at least one by the life history of the dominants (California annual grass series). There are also "mixed series" where the dominance rule is relaxed to admit various dominance combinations of a small set of species (mixed conifer series). Each series is presented on a page or two in a systematic format that includes a brief description, geographical distribution (by a system very similar to, but not identical with, that used in the new *Jepson Manual*), a table that equates common and scientific names of species mentioned, a list of published quantitative descriptions of the series.

Many series descriptions also include lists of described "associations". This level of the hierarchical system, the only one other than series that is explicitly identified or discussed in the volume, is defined as a sub-unit of a series characterized by the presence or absence of particular species, usually in lower canopy strata (as in the incense cedar/twayblade association of the incense cedar series), but sometimes within the same stratum as the dominants (e.g., the incense cedar-Douglas fir association). There are many unanswered questions about the association. How, for example, in a hierarchical system, can an association be assigned to more than one series, as the authors state? Why is it that, in some instances, an association will have the same name as the series? The chamise-hoaryleaf ceanothus series has two named associations, one of which is the chamise-hoaryleaf ceanothus association. This seems odd. Is the same-name association a catch-all for everything that is not in the other associations? In another puzzling case, the dune lupine-goldenbush series has three associations, the heather goldenbush association (does this mean that no *Lupinus* is present?), the dune lupine association (no *Isocoma* or *Ericameria* is present?), and dune lupine-heather goldenbush association (everything else)? The many inexplicable instances in the implementation of the associations cry out for a fuller discussion in the introduction.

Dominance relations are the most fundamental aspect of the entire classification. It is therefore perplexing that dominance is only vaguely defined. A dominant is "an abundant species with high crown cover, especially in relation to other species in the stand". This leaves the reader in confusion as to whether dominance is an absolute or relative measure and exactly what "high" means. Study of various series suggests that relative cover is what is used in practice. Another key word in the SKW system is "important", which is applied to species that are not dominant, but are, well, important. As the lack of specific numbers to define these terms is too conspicuous an omission to be an error, one must assume that the authors preferred the flexibility afforded by nonquantitative definitions.

The flexibility theory is given weight by noting that, in some instances, quantitative criteria are provided in series descriptions—suggesting that more precise definitions of dominance are optional. Thus, for example, red shank series consists of stands having >60% red shank cover, but if red shank is 30 to 60% and another species within the same range, it is placed in a series defined by red shank and that other species, such as the red shank-chamise series. These quantitative guidelines do not eliminate all the problems. If stand A were 30% red shank and 55% chamise it would be classified as red shank-chamise. Referring to the chamise series, we learn that any stand with >60% chamise is in the chamise series, so that if stand B had 38% red shank and 62% chamise it would be the chamise series, even though the ratio of red shank to chamise and the cover of red shank would both be higher in B than in A. The system also opens the door to the peculiar situation in which there might be 30% red shank, 30% chamise, and up to 40% of some other species. Presumably this series would be called red shank-chamise, even though the third species was as abundant or more abundant than the two defining species.

The SKW system is unequivocally on the side of "describe what you see" and

rejects notions of speculating about "potential vegetation", as has been done in many vegetation mapping efforts. This solves one set of problems but creates others. In many circumstances, post-fire shrub vegetation is dominated by herbs and post-crown fire forest vegetation by shrubs. Surely the authors are not suggesting that such rapid and highly predictable successions are to be ignored? Yet no guidance is given on how to deal with them.

Because the series is at the heart of the SKW system, one might expect that the process by which series are defined would be explained in some detail. This is not the case. But the presence of the CNPS sampling protocol in an appendix and the comment in the text that the process of vegetation classification is "often long and detailed" implies that the authors have used or at least favor quantitative sampling and rigorous analysis for the description of series. This is underscored by the citations in the series descriptions of articles that present quantitative data. But the citations are highly diverse with respect to methodology, purpose, and comprehensiveness, and therefore it seems that the delineation of series cannot always have been based on "long and detailed" quantitative analysis. There is the suspicion that most series in the present volume were established subjectively and did not involve an analytical process analogous to that used by systematists to demonstrate that a new species is sufficiently distinct from existing species to deserve recognition.

The series is not, however, the only element of the system presented. They recognize three other categories similar to series: unique stands, habitats, and vernal pools. The "vernal pool" category is the most anomalous. The authors say that there is disagreement as to whether vernal pools should be treated from the vegetation or the ecosystem viewpoint, as though these were non-overlapping alternatives. They opt for the ecosystem view, which is odd, given that they have said earlier that floristics and rarity are the important factors. But what they call an ecosystem view is really more a biogeographical approach, since they divide the vernal pools into regional groups (e.g., Santa Rosa plateau vernal pools) and each group is described by the presence of particular plant species or genera. This will perhaps draw fire from the growing vernal pool invertebrate animal constituency, who argue that vernal pools with sparse or even no vascular plant cover are nonetheless vernal pools if they support characteristic animal assemblages. But more serious is the fact that providing vernal pools with their own unique category leaves it unclear where vernal pools fit, if anywhere, in the hierarchical scheme, and in series in particular. Using the series keys on southern California, vernal pools could lead to the spikrush series or the quillwort series for some pools or to totally inappropriate series for others. The keys don't direct the novice to "vernal pools", so anyone who uses the key at a small scale, which seems to be permitted in SKW, is in trouble unless they have a pretty good idea of what a vernal pool is independent of SKW. This raises the question: Why weren't vernal pools treated as series or perhaps in some cases as associations within the series in which they are found (annual grassland, chaparral, oak woodland)? It can't be because they are too small, since as we have seen, duckweed and quillwort patches can be series. It certainly isn't because the vegetation is not distinct, because there are many endemic species in vernal pools and the life histories and life forms are highly distinctive. The suspicion arises that this ambiguous treatment of vernal pools is explained by the recognition that if small habitats like vernal pools are to be included within the series system they either must be contained within other series (which might be politically dangerous) or that objective analysis will produce a proliferation of "series" along the lines of the chamise-red shank situation described above, only with many more potential dominants with much more restricted geographical ranges. If there is to be a set of series for pools, why not, for example, series for rock faces like the *Selaginella-Dudleya* series? The authors seem to be reluctant to promote that kind of fine-scale application of series, but are also reluctant to relegate a vegetation type of such conservation importance to a lower level of the hierarchy.

The purpose of the "habitat" designation is somewhat clearer. These are aggre-

gated vegetation types felt to deserve recognition but about which there is insufficient information to justify subdivision into series. Such problems seem to occur more frequently in the mountains, since six of the seven "habitats" are montane, and only one, "fen", is not specifically linked to mountains but probably will mostly be at higher elevations, except in the north coastal regions. The habitat designation raises questions about the seriousness of the commitment to a hierarchical approach. Habitats are a kind of interim higher unit. But if the SKW system had taken a top-down approach, there would be no need for interim treatment. Thus "montane meadow" could contain all future series corresponding to whatever criteria define this unit. It is not clear that this will be the case. But in contrast to the reluctance to define higher categories, SKW sees no problem with identifying lower units. They present quite long lists of associations contained within several of the habitat types. This raises a question: Is it possible in an objective hierarchical system to identify lower elements before the higher units are defined? Using the authors' own genus-species analogy for their hierarchy, it seems to be like identifying species without a concept of the genus.

"Unique stands" is the third ad-hoc grouping of vegetation types containing 24 vegetation units. The argument for the utility of this category is based on the authors' belief that recurrence of a particular species composition at multiple sites is fundamental to the definition of a series. They note that every stand of vegetation is unique, but evidently feel that some are more unique than others—thus this grab-bag of series wannabes that fail the "redundancy" test. Lack of redundancy seems to be particularly acute among California conifers (12 of the 24 unique stands) and of the rarer woody species in general (16 of 24). Rarity seems to be problematical because it reduces the number of sites at which a species is found. But beyond this, most of the unique stands are judged to be situations in which a single species pops up in vegetation that otherwise could be assigned to existing or future series. For example, SKW relegates Tecate cypress stands to "unique" status, but creates a series for Sargent cypress. A Tecate cypress stand looks pretty much like a Sargent cypress stand. So what is different? The only obvious difference is that Sargent cypress has a much broader range in the United States. Tecate cypress occurs in only two counties in the U.S. and has many fewer stands. Though one may suspect that range is a factor, that is not identified as the problem. The authors note that Tecate cypress "associates with local series rather than forming one". Thus Tecate cypress, which is locally dominant, flunks the series test by not being more discriminating in the species with which it associates. Evidently some unspecified degree of fidelity between a dominant and its co-occurring species is necessary and primary. We may speculate why Tecate cypress, which has probably been around for at least as long as Sargent cypress, seems to have been less able to form stable phyto-relationships than its sister taxon to the north. As with "vernal pools", unique stands seem to be an expedient indicating indecision or uncertainty on the part of the authors. They can't ignore these visually and floristically obvious phases of the vegetation, they don't feel they can make them a series, but neither are they willing to take the plunge and relegate them to a lower status of the hierarchy, presumably because that would violate the dominance principle and perhaps insult the local constituencies for these vegetation types.

The SKW scheme, like many other attempts at vegetation classification, places a heavy reliance on keys. It is assumed that the user has identified a "homogeneous" (not defined) area of vegetation (no scale specified) and either has actually sampled the area presumably following the CNPS guidelines or is experienced enough to estimate the various features needed visually. The reasonable assumption that the user has accurate identifications for all of the more abundant species in the highest canopy is also made. The first decision required by the key is whether the stand is dominated by herbs, shrubs, or trees. These are defined in the glossary in rather general terms. There is no fixed height definition for shrubs and trees. Shrubs are "short" when fully grown and tend to be multiple-stemmed, and trees are "tall" when fully grown

and tend to have one stem. The keys then subdivide the vegetation on the basis of many features, including growth form, taxonomic groupings, biogeographical groupings (e.g., "coastal scrub species"), and the degree of expression of dominance of the dominant species. Examples of choices are "Grasses dominant", "A *Cercocarpus* species not important", "Chaparrals where one species dominates".

It is clear that thought has gone into the keys, but they do not always function well. They differentiate the series primarily on the basis of presence, importance, and dominance of species, genera, growth forms (trees, shrubs, aquatics), life history types (evergreen), or, in a few cases, structural or biogeographical groups ("desert scrub species", "coastal scrub species"). Because of the lack of strict definitions of most of these terms, use of the keys will be most comfortable for those who are predisposed to fuzzy logic. Strictly binary thinkers will be frustrated trying to decide, for example, if species are "conspicuous" versus "not conspicuous".

Many ecologists will be vexed that a single series includes stands that occur on dramatically different substrates and in completely different geomorphological settings, and that successional stages are not recognized or dealt with in the system. To believers in continuous variation it is hard to overlook the fact that many, probably most, series grade into others and that boundaries are likely drawn arbitrarily.

In fairness to the authors, it must be noted that they do not present their system as a finished product. On the contrary, they see this publication as only the first iteration of an evolving program. They expect that other series will be defined, and though they don't say so, presumably they would not be averse to dropping or changing existing series or associations. The full hierarchy of vegetation will presumably also be presented sometime in the future, though this is not promised. But it is clear that they are assuming that change is going to be evolutionary, not revolutionary and that their newly hatched manual is a well adapted organism, and not a hopeful monster. But will SKW survive through the 21st century?

There are reasons to be skeptical. There is nothing in vegetation classification remotely as basic and compelling as the concept of genetic relatedness by virtue of inheritance in systematics. There is no "correct" answer for the question of how to deal with temporal and spatial variation in vegetation. It depends on the purpose. The vegetation classification that does the best job of distinguishing elements of the landscape worthy of preservation is unlikely to be the best system for describing the dynamic relations between different states of the vegetation, or to provide the units that are the best for mapping vegetation for management purposes. It is to be noted that the authors do not necessarily claim universality for their system, but they also fail to make a convincing case that their collection of series and associations constitutes the best or even an acceptably good system compared to some other for the primary purpose of informing conservation and management activities.

Most troubling is the underlying assumption of discontinuous variation. Bloody battles were fought in plant ecology from the 1930s through the 1960s over the fundamental nature of the plant community. Many of us thought that the Gleasonian individualistic hypothesis was the clear winner, and relegated typological thinking about vegetation to the dustbin of history. This smug confidence was premature, as SKW shows. The authors tip their hat toward Gleason in the introduction, but in the implementation the underlying paradigm clearly is one of discontinuous variation. The seem to say "California vegetation is complex, but it is patchwork with a relatively small number of kinds of patches. With enough study, we will be able to figure out how many kinds of patches there are". They don't think we have identified them all yet, but they are confident that in principle we will. They encourage the idea that "discovery" of new series and associations and publication of data describing them is an important task. This raises a frightening image of scholarly publications clogged with studies like "Seventeen new associations in the Mojave yucca series". There is, of course, a need for more and better data on the vegetation of California, but the decisions about where to spend the effort and how to design the studies should not be guided by the needs of vegetation taxonomy.

It is useful to have a compendium of the different kinds of vegetation. SKW provides a valuable summary of the state of our knowledge and useful summary of one view of how many different kinds of vegetation we have. Its scholarship is impressive, but it is not the last word on how we should organize and understand the complexity of California vegetation. I can recommend buying the volume, but not the imposition of the system that it describes.

—PAUL H. ZEDLER, Biology Department, San Diego State University, San Diego, CA 92182-0057

Niebla and Vermilacinia (Ramalinaceae) from California and Baja California BY RICHARD W. SPJUT. Sida, Botanical Miscellany No. 14, Botanical Research Institute of Texas, Inc. 209 pp.

This monograph includes keys and descriptions for 71 North American species and one variety of *Niebla* and *Vermilacinia*, fruticose lichen genera, of which 53 species and the variety are new. These genera include highly polymorphic taxa that have been segregated from *Ramalina* sensu lato on the basis of vegetative anatomy and chemistry. *Niebla* sensu lato was proposed by Rundel and Bowler (1978) on the presence of medullary chondroid strands in most, abundant black pycnidia, and shared chemical features. *Vermilacinia* was segregated from *Niebla* sensu stricto by Spjut (1995), on the basis of distinctive secondary metabolites, and the lack of medullary chondroid strands and the reticulate surface ridging of *Niebla* sensu stricto. Included in *Vermilacinia* are species aggregates formerly called *Niebla combeoides* and *N. ceruchis*, while *Niebla* sensu stricto includes segregates from the former *N. homalea*. The many new species help to make sense of the highly polymorphic populations encountered in nature. About 2000 specimens were examined, mostly from the author's collections but also representing sizeable holdings from COLO, FH, US, and the C. Bratt private collection.

The North American distribution of the two genera is centered in the fog zone and Mediterranean California climate zone of the Pacific coast of California and Baja California, with some species extending as far north as San Juan Island, Washington, and a few others in South America, the Mediterranean, and Macaronesia. Twenty species of *Niebla* and 18 species of *Vermilacinia* are reported here for the United States. Those outside North America are not considered here.

Both morphologically based and chemically based keys are provided. The morphological key, while having some ambivalent dichotomies, is generally workable after some effort in learning how specific terms are used by the author. Detailed morphological descriptions are given for each species, as well as chemistry, distributions, and lists of representative specimens. Some species pairs apparently differ only chemically. Terminology is complex but explained in detail in a section of the text as well as in a glossary. A few terms still appear ambiguous: "glossy" versus "glabrous, creamy" surface, for example.

It is a pleasure to encounter a lichen monograph that contains numerous illustrations of the "plants", apart from those showing their internal structure and chemistry. There are 66 color photographs, most showing close-up views of individual organisms, but also several showing habitat. One or more excellent-quality black and white photographs with scale is provided for each species. Drawings included in the keys, however, are variable in quality. Maps show floristic provinces and collecting locations for each species. Many endemic taxa are included; endemics are rather unusual among lichens.

Richard Spjut has produced a workable treatise on two difficult genera of lichens, which have seemed intimidatingly polymorphic. He has brought together a useful compilation of the current status of information about *Niebla* and *Vermilacinia*, as well as on the climatic types, vegetation zones, and phytogeography of the regions

of interest. New range extensions in distributions of individual species are likely to be added for many taxa, particularly in the Channel Islands of California. Some of the chemical species may not be acceptable to all.

This monograph is essential for any lichenologist who collects or works with lichens of the Pacific coast of the Americas. It also is highly recommended to ecologists and systematists interested in desert and fog zones. The moderate price of the paperback makes this book accessible to nearly everyone, including students.

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—SHIRLEY C. TUCKER, Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106.

California's Forests and Woodlands: A Natural History, BY VERA R. JOHNSON. 1994. The University of California Press, Berkeley. x+222 pages. Hardcover \$30. ISBN 0-520-08324-5.

The title, *California's Forests and Woodlands*, sounds, at first hearing, like one of those encyclopedic tomes that culminates a researcher's career. Perhaps that was hopeful thinking on my part (wouldn't it be great to have such a reference?), but this readable, 222-page book is closer in spirit and substance to *An Island Called California* (Bakker 1984). The book's stated purpose is "to bring hours of pleasurable, informative reading and an increased awareness of the priceless heritage of California's forests and their wildlife", and this it does quite well.

Johnston's book centers around conifers. This initially seemed odd to me, since I grew up in southern California, where oaks dominate, but Johnston argues that a) most of California's forests and woodlands are dominated by conifers, b) California has a great (unrivaled?) diversity of conifers, and c) oak woodlands and forests are already covered in the *Oaks of California* (Pavlik et al. 1991). In any case, conifers dominate the book's structure, which is organized around the different coniferous forests of California. Each chapter covers a different forest type, with topics including redwood forests, north coastal forests, mixed douglas-fir forests, closed-cone pines and cypresses, foothill woodlands, giant sequoia groves, upper montane and subalpine forests, and pinyon pines/juniper woodland. The intricacies of the Klamath region are segregated into their own chapter. Rounding out the book are an introductory chapter on identifying conifers and a concluding chapter on the ongoing conservation problems faced by California's forests and tips on how to get involved in the battle.

Each of the main chapters starts with the dominant conifers and works outwards, covering species ranges, associated plants, ecology, and the like, painting a picture of each forest and its ecological quirks. Animals are brought into the picture, so that the forests become populated with owls and rodents, insects, and reptiles. Vignettes follow, depicting interesting aspects of each forest's ecology (such as the Douglas-fir canopy ecology discovered by researchers at Oregon State). Interspersed with these vignettes are histories of these forests and observations from historical figures such as Muir and Nuttall, along with discussions of the environmental problems the forests

currently face. While these treatments may seem slightly simplistic to an expert, they are appropriate in this book, which is definitely geared towards the interested non-specialist.

Most of the book is understandably focused on northern California and the Sierra, but the conifers of southern California do get some space. In fact, one of Johnston's accomplishments is that she apparently included every California conifer in her book. As for utility, this is the kind of book that would make an excellent present, especially to people who like to hike and want to know more about their surroundings. It would also be useful as a text for natural history or environmental studies classes, especially in the northern and central parts of the state.

LITERATURE CITED

- BAKKER, E. 1984. An island called California. Berkeley and Los Angeles, University of California Press.
- PAVLIK, B. M. et al. 1991. Oaks of California. Sacramento, Cachuma Press and the California Oak Foundation.

—FRANK LANDIS, Department of Botany, University of Wisconsin-Madison, 430 Lincoln Dr., Madison, WI 53706.

ANNOUNCEMENT

THE 1997 JESSE M. GREENMAN AWARD

The 1997 Jesse M. Greenman Award has been won by Elena Conti for the publication "Circumscription of Myrtales and their relationships to other rosids: Evidence from *rbcL* sequence data", coauthored by E. Conti, A. Litt, and K. J. Sytsma, and published in *American Journal of Botany* 83(2): 221–233 (1996). This study is based on a Ph.D. dissertation from the University of Wisconsin under the direction of Dr. Kenneth J. Sytsma.

The Greenman Award, a certificate and a cash prize of \$1000, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation published during the previous year. Papers published during 1997 are now being accepted for the 30th annual award, which will be presented in the summer of 1998. Reprints of such papers should be sent to Dr. P. Mick Richardson, Greenman Award Committee, Missouri Botanical Garden, P. O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. In order to be considered for the 1998 award, reprints must be received by 1 June 1998.

ERRATA

In the Review of *California Plant Community Information System*, by Steven Hartman (Madroño 43(2): 392), the address supplied was incorrect. The address has since changed to 6117 Reseda Blvd. Suite H, Reseda, CA 91335.

In "*Romanzoffia thompsonii* (Hydrophyllaceae), a new species from Oregon", by Vernon M. Marttala (Madroño 43(2): 404–414), Table 1, under Habitat Syndrome #1 should read "cences $\geq 2 \times$ to 1.5–2".

MADROÑO, VOL. 44, NO. 2, p. 222, 1998

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THE SYSTEMATICS OF ANNUAL SPECIES OF
MALACOTHRIX (ASTERACEAE: LACTUCEAE)
ENDEMIC TO THE CALIFORNIA ISLANDS

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ABSTRACT

A taxonomy based primarily on phenetic evidence is proposed for the annual taxa of *Malacothrix* DC. endemic to the California Islands, California. Field studies, herbarium collections, and growth chamber progenies provided information about chromosome numbers, breeding systems, the presence or absence of isolating mechanisms between taxa, comparative morphology, and distributions. New taxa described are *Malacothrix foliosa* ssp. *crispifolia* ($2n=14$), *M. f.* ssp. *philbrickii* ($2n=14$), *M. f.* ssp. *polycephala* ($2n=14$), and *M. junakii* ($2n=28$). Kept at the species level are *M. indecora* ($2n=14$), *M. insularis* ($2n$ =unknown), and *M. squalida* ($2n=28$). Also discussed are possible relationships between the insular endemics and *Malacothrix coulteri* ($2n=14$) and *M. incana* ($2n=14$), two species that occur both on the California Islands and on the mainland.

Malacothrix DC. comprises annual and herbaceous perennial plants that occur exclusively in the western United States and northern Mexico, except for two species that also occur in Argentina and Chile. The most recent monograph recognized 23 taxa (Williams 1957), and Davis (1993) has updated the taxonomy of taxa occurring in California. During the taxonomic history of the genus, there has been general agreement about the circumscription of a majority of species. Notable exceptions are the annual species endemic to the California Islands, originally published as follows: *Malacothrix foliosa* A. Gray (1886, San Clemente Island); *M. indecora* Greene (1886, Santa Cruz Island); *M. insularis* Greene (1885, Los Coronados Island); and *M. squalida* Greene (1886, Santa Cruz Island). More recently, annual *Malacothrix* also have been collected on Anacapa, San Miguel, San Nicolas, Santa Barbara, and Santa Rosa islands. Most of these collections have been referred to the original four species whose taxonomy has received a variety of treatments. For example, Williams (1957) reduced *M. indecora* and *M. squalida* to varietal rank under *M. foliosa* and combined *M. insularis* with *M. foliosa* var. *foliosa*. Ferris (1958) treated *M. squalida* as a variety of *M. insularis* and retained *M. foliosa* and *M. indecora* as species. Munz (1974) accepted specific status for *M. foliosa* and stated, "Two other spp. have been proposed and variously combined as vars., all of these occurring only on the islands off our coast and to me quite mixed up as to separating characters and distribution."

This study was undertaken to resolve the taxonomic disagreements noted above; its primary focus is on the annual taxa of *Malacothrix* endemic to the California Islands. Also included in the study are two taxa occurring both on the islands and on the mainland. The first is *Malacothrix incana* (Nutt.) Torrey & A. Gray, a diploid ($2n=14$) perennial occurring in sand dune areas of coastal mainland California in Santa Barbara and San Luis Obispo counties. *Malacothrix incana* also is an element of sand dunes on San Miguel, Santa Cruz (not recently seen there), Santa Rosa, and San Nicolas islands. It was included in the study because it is similar to the annual insular endemics in several aspects of floral and leaf morphology. Also included, because of morphological similarities to *M. insularis* and *M. squalida*, is *Malacothrix coulteri* A. Gray, a diploid ($2n=14$) annual occurring in Arizona, California, Nevada, Utah, Argentina, Chile, and northwestern Mexico. It was collected on Santa Cruz and Santa Rosa islands in the past (as *M. coulteri* var. *cognata* Jepson), but not since 1932.

Initial findings of consistent patterns of morphological and physiological variation within the study group (henceforth referred to as the *M. foliosa* complex) developed from studies of growth chamber progenies grown under similar light, temperature, and soil conditions (see Davis and Philbrick 1986 for propagation methods). Voucher specimens are deposited in Davies Herbarium (DHL), University of Louisville. Progenies grown from wild achenes of all taxa except *Malacothrix insularis* Greene were available, as well as progenies from self-pollinations, intrataxon pollinations, and intertaxon pollinations.

For breeding system determinations, a plant was considered to be self-incompatible if no pigmented/filled achenes were produced from at least three self-pollinations or in undisturbed heads, and if crosses with other plants of the same taxon produced normal numbers of pigmented/filled achenes.

No information regarding the presence of self-compatible or self-incompatible plants in natural populations was gathered because no island trip was longer than four days, and ten days are required for fruit set to occur following pollination. Pollination systems appeared to be very effective in all natural populations, and high percentages of full/pigmented achenes were noted in all taxa during collections of achenes in the field. On San Clemente Island, for example, mature flower heads of *Malacothrix foliosa* ssp. *foliosa* were collected from 14 different plants. Percentages of full/pigmented achenes per head were 95–100, and the potential numbers of achenes per head were 39–112. In natural populations, insects are the most important pollinators for all taxa, and a study on San Miguel Island by Miller and Davis (1985) found that flower heads of *Malacothrix incana* are visited by a suite of generalist bees, small beetles, true bugs,

and a few flies. The most frequently seen pollinator was *Agapostemon texanus* Cresson. The large metallic-green female was often found crawling all over the large flower heads. This same pollinator was seen on both *M. foliosa* ssp. *polycephala* and *M. incana* on San Nicolas Island during a study of hybridization between the two species.

The presence or absence of isolating mechanisms between taxa was investigated experimentally in growth chamber progenies by comparing the results from intrataxon crosses with those from intertaxon crosses with respect to the following: quantity and quality of fruit set, percentage seed germination, patterns of seedling growth and development, percentage stainable pollen, and chromosomal associations at diplonema, diakinesis, and metaphase I of meiosis.

Field studies were conducted during visits to Anacapa Island (1982, 1992), San Clemente Island (1985), San Miguel Island (1984), San Nicolas Island (1984–1988, 1993), Santa Barbara Island (1982), and Santa Cruz Island (1985, 1991).

Morphological data were collected from herbarium specimens deposited in the following herbaria: CAS, DAV, DS, GH, JEPS, K, LA, LAM, MO, ND, NDG, NY, OBI, POM, RSA, SBBG, SBM, SD, TEX, UC, UCSB, UNM, US. All of the collections of *Malacothrix* cited in Raven (1963), Foreman (1967), Philbrick (1972), Wallace (1985), and Junak et. al. (1995) were analyzed.

The taxonomy proposed in this paper is based primarily on phenetic evidence. Cluster analysis of 33 quantitative floral and vegetative characters (Fig. 1) provided a picture of over-all resemblances between taxa in the study, and assisted in making taxonomic decisions. Cluster methods were performed on a personal computer using NTSYS-PC, version 1.6 (Rohlf 1990). A similarity matrix was constructed using the product-moment correlation method on unstandardized mean values, and the phenogram was obtained using the unweighted pair-group arithmetic averages method (UPGMA).

A summary of the new classification of the plants covered in the study is given in Table 1, together with the old classification and brief information about distributions, reproductive biology, and chromosome numbers (see Fig. 2 for geographic distributions).

All of the taxa grown in growth chamber progenies from wild fruit or fruit from sister crosses within a taxon were true-breeding, and patterns of morphological variation observed in natural populations were comparable to patterns found in growth chamber progenies. The different taxa are most consistently distinguishable on the basis of differences in cauline leaf morphology (Fig. 3) and size differences in some quantitative floral traits (Table 2). Differences between taxa in quantitative floral traits are easily seen in the field and in growth chamber progenies, but are difficult to assess in her-

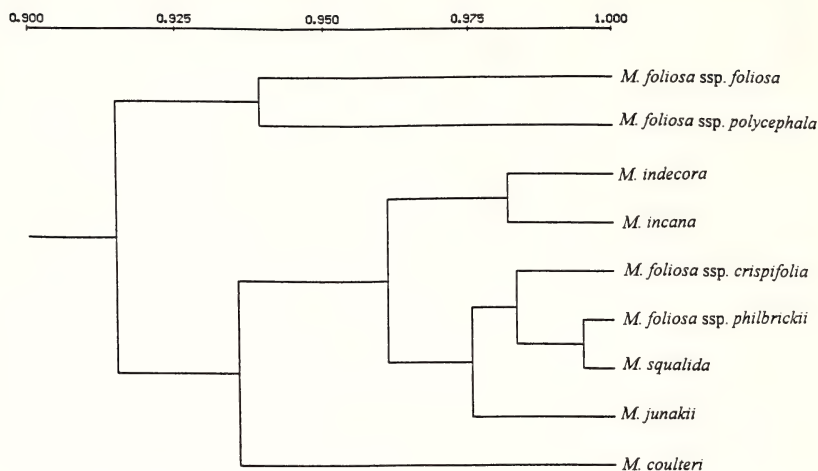


FIG. 1. Phenogram showing the clustering of taxa of the *Malacothrix foliosa* complex resulting from UPGMA cluster analysis carried out on NTSYS (Rohlf 1990) using means of 33 quantitative vegetative and floral traits (scale = correlation coefficients). Cophenetic analysis indicated that the phenogram is a good fit to the original data set. *Malacothrix insularis* was not included because of insufficient data from dried specimens, and no information from living plants.

barium specimens. This may account for some of the taxonomic confusion in the past when few collections were available for study.

Diploid insular endemic taxa comprising only self-compatible, strongly self-pollinating plants (CRI, IND, POL) have shorter corollas, stamens, and involucres than diploid members of the *M. foliosa* complex that comprise both self-compatible and self-incompatible plants (FOL, INC, PHI) (Table 2). In the latter group, I have been unable to find any differences between self-compatible plants and self-incompatible plants. In comparative size of diagnostic quantitative floral traits, FOL, INC, and PHI are similar to other taxa of *Malacothrix* that have been found to comprise outcrossing plants. The polyploid SQU and the presumptive polyploid INS have the general floral dimensions of an outcrosser, but SQU comprises only self-compatible, self-pollinating plants. The diploid COU and the polyploid JUN are somewhat intermediate in size between other known inbreeders and outcrossers in some quantitative floral traits (Table 2).

Biological barriers interfering with gene exchange between taxa of the *M. foliosa* complex and other predominately mainland taxa have been found in growth chamber studies. For example, it has been very difficult to obtain filled achenes from cross-pollinations between members of the *M. foliosa* complex (COU, CRI, FOL, INC, IND, JUN, PHI, POL, SQU) and any predominately mainland taxon,

TABLE 1. OLD CLASSIFICATION, AND NEW CLASSIFICATION. DISTRIBUTIONS, BREEDING SYSTEMS, AND CHROMOSOME NUMBERS OF TAXA OF THE *M. FOLIOSA* COMPLEX. Names of taxa are represented in the text by the first three letters of specific or subspecific epithets as listed in column 2. All of the taxa are annuals except *M. incana*.

| Old classification | New classification | Distribution | Breeding system | Chromosome number |
|---------------------|---|---|---|-------------------|
| <i>M. coulteri</i> | <i>M. coulteri</i> (COU) | Mainland; formerly on Santa Cruz & Santa Rosa Islands | Self-compatible & strongly self-pollinating | $2n = 14$ |
| <i>M. foliosa</i> | <i>M. foliosa</i> ssp. <i>crispifolia</i> (CRI) | East & west Anacapa Island | Self-compatible & strongly self-pollinating | $2n = 14$ |
| | <i>M. foliosa</i> ssp. <i>foliosa</i> (FOL) | Widespread on San Clemente Island; formerly on Los Coronados Island | Both self-compatible & self-incompatible | $2n = 14$ |
| | <i>M. foliosa</i> ssp. <i>philbrickii</i> (PHI) | Widespread on Santa Barbara Island | Both self-compatible & self-incompatible | $2n = 14$ |
| | <i>M. foliosa</i> ssp. <i>polycephala</i> (POL) | Widespread on San Nicolas Island | Self-compatible & strongly self-pollinating | $2n = 14$ |
| <i>M. incana</i> | <i>M. incana</i> (INC) | Currently mainland and insular | Self-compatible & self-incompatible | $2n = 14$ |
| <i>M. indecora</i> | <i>M. indecora</i> (IND) | San Miguel, Santa Cruz & Santa Rosa Islands | Self-compatible & moderately self-pollinating | $2n = 14$ |
| <i>M. insularis</i> | <i>M. insularis</i> (INS) | Rare on Los Coronados Island | Not known | Not known |
| | <i>M. junakii</i> (JUN) | Rare on middle Anacapa Island | Self-compatible and moderately self-pollinating | $2n = 28$ |
| <i>M. squalida</i> | <i>M. squalida</i> (SQU) | Santa Cruz & middle Anacapa Islands | Self-compatible & strongly self-pollinating | $2n = 28$ |

and few artificial hybrids have been available for study. All hybrids produced have been sterile (pollen stainability generally $<10\%$), and abnormal chromosome associations are generally found in meiosis. Likewise, growth chamber studies have found that intertaxon crosses between predominately mainland taxa also produce hybrids rarely, that these hybrids are sterile (stainable pollen $<50\%$), and that ab-

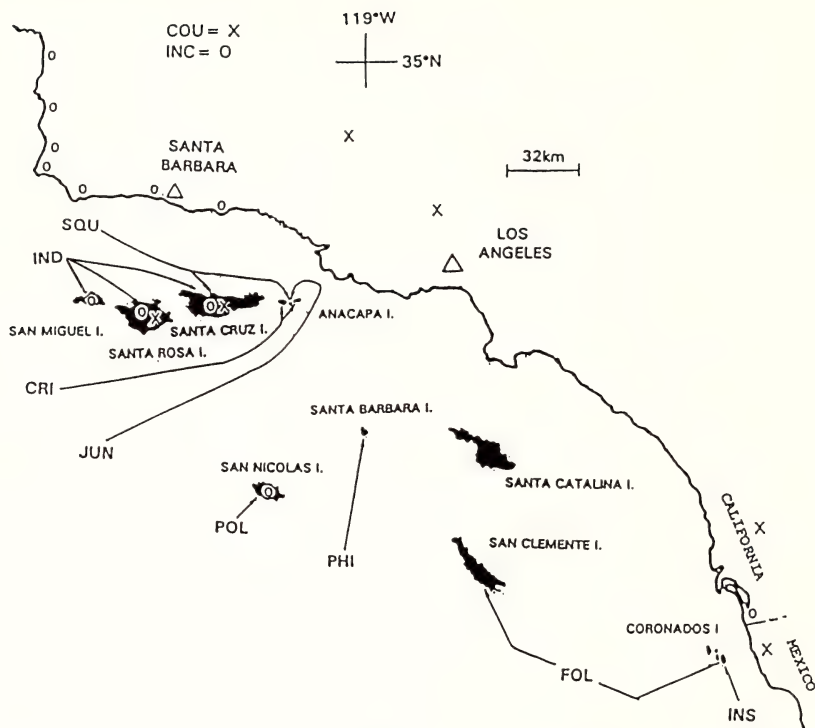


FIG. 2. Distribution of taxa of the *Malacothrix foliosa* complex on the California Islands and adjacent mainland (COU = *M. coulteri*, CRI = *M. foliosa* ssp. *crispifolia*, FOL = *M. f.* ssp. *foliosa*, INC = *M. incana*, IND = *M. indecora*, INS = *M. insularis*, JUN = *M. junakii*, PHI = *M. f.* ssp. *philbrickii*, POL = *M. f.* ssp. *polycephala*, SQU = *M. squalida*).

normal chromosome associations may be found in meiosis (Davis 1993).

In contrast, growth chamber hybridization studies indicate that all but one of the diploid members of the *M. foliosa* complex (CRI, FOL, INC, IND, PHI, POL, but not COU) are generally interfertile. Fruit set was normal in all intertaxon crosses except PHI \times IND where $<5\%$ of the achenes were filled/pigmented in a majority of cases when self-incompatible plants of PHI were used as the female parent (percentage of stainable pollen of F_1 hybrids from PHI \times IND was $>90\%$). Germination rates were normal for seeds from all intertaxon crosses including PHI \times IND, growth and development were apparently normal, a majority of hybrid combinations displayed hybrid vigor, and all growth chamber hybrids flowered normally. Meiosis in all intertaxon hybrids was apparently normal, and chromosome segregation was normal in metaphase I and II. Mean

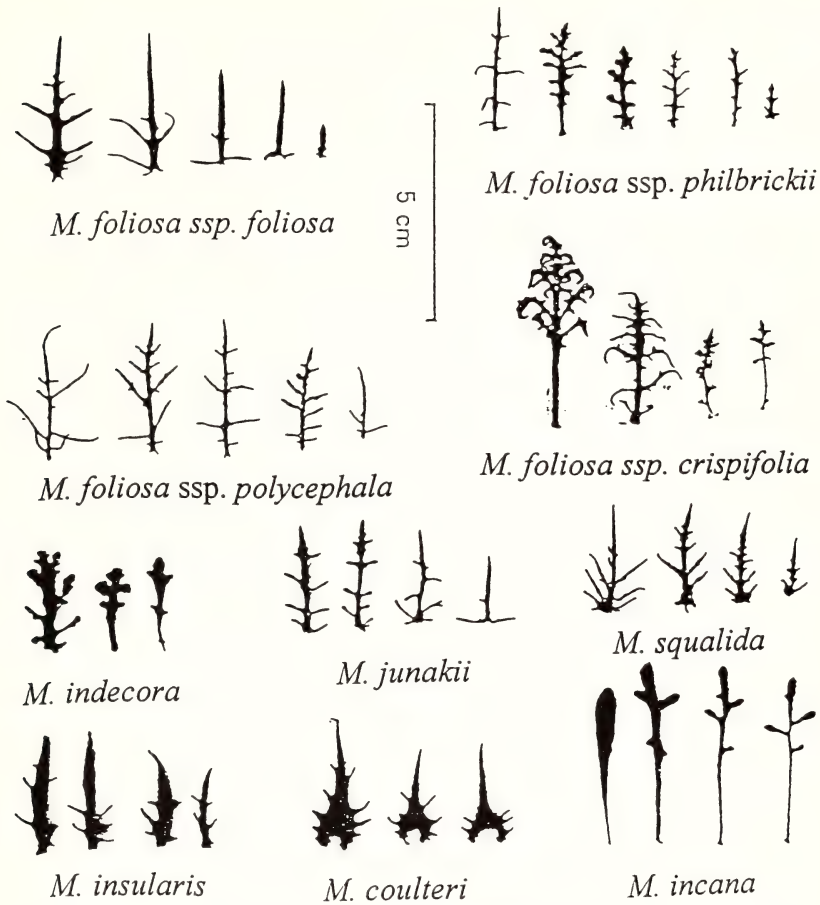


FIG. 3. Silhouettes of cauline leaves of taxa of the *Malacothrix foliosa* complex arranged with progressively more apical leaves to the right.

percentages of stainable pollen in F_1 and F_2 hybrids did not differ significantly ($P > 0.05$, Students t-test) from mean stainable pollen percentages in plants grown from wild fruit or from intrataxon crosses, except in some of the F_1 hybrids from $INC \times IND$ which had stainable pollen $< 40\%$.

In contrast, the two polyploid members of the *M. foliosa* complex (JUN, SQU), and the diploid COU are reproductively isolated from the above diploid taxa of the *M. foliosa* complex and from each other (Table 3).

Geographic isolation or absence of sympatry currently helps preserve the integrity of interfertile taxa of the *M. foliosa* complex. Islands occupied by a single taxon include San Clemente (FOL),

TABLE 2. VARIATION IN QUANTITATIVE FLORAL FEATURES OF TAXA OF THE *M. FOLIOSA* COMPLEX (GIVEN ARE RANGE, MEAN \pm STANDARD DEVIATION; N = NUMBER OF INDIVIDUAL PLANTS STUDIED).

| Taxon | Ligule exsertion | | | | Ligule length (mm) | Ligule width (mm) | Stamen length (mm) |
|--|---------------------|---------------|----------------|---------------|--------------------|-------------------|--------------------|
| | Corolla length (mm) | (mm) | (mm) | (mm) | | | |
| <i>M. coulteri</i> | 8.8-12 | 1.9-5 | 5.2-7.2 | 1.3-2 | 4.8-6.2 | | |
| N = 6 | 10.8 \pm 0.8 | 3.3 \pm 1.1 | 6.1 \pm 0.8 | 1.6 \pm 0.3 | 5.8 \pm 0.6 | | |
| <i>M. foliosa</i> ssp. <i>crispifolia</i> | 6.1-10 | 2.7-3.9 | 4.6-6.2 | 2.2-2.7 | 4.3-6 | | |
| N = 16 | 8.9 \pm 0.8 | 3.2 \pm 0.3 | 5.5 \pm 0.7 | 2.4 \pm 0.2 | 5.4 \pm 0.4 | | |
| <i>M. foliosa</i> ssp. <i>foliosa</i> | 10-16 | 4.6-7.9 | 6.7-12.1 | 2-4 | 5.3-8.1 | | |
| N = 34 | 12.9 \pm 1.4 | 6.6 \pm 1.0 | 8.7 \pm 1.1 | 3.3 \pm 0.4 | 6.7 \pm 0.7 | | |
| <i>M. incana</i> | 10.8-20 | 5.2-9 | 7.5-12 | 2.2-3.1 | 7-12 | | |
| N = 23 | 16.46 \pm 1.3 | 6.7 \pm 1.3 | 10.0 \pm 0.9 | 2.9 \pm 0.2 | 9.8 \pm 1.0 | | |
| <i>M. indecora</i> | 4.5-8 | 1.3-3.3 | 2.7-4.6 | 1.5-2.5 | 3.4-5.4 | | |
| N = 28 | 6.9 \pm 0.8 | 1.9 \pm 0.5 | 3.8 \pm 0.5 | 2.2 \pm 0.2 | 4.6 \pm 0.5 | | |
| <i>M. insularis</i> | 11.7-15 | 3.5-5 | 7.5-9.5 | 2-2.5 | 6-9 | | |
| N = 11 | 12.3 \pm 1.1 | 4.6 \pm 0.7 | 8.4 \pm 0.6 | 2.2 \pm 0.1 | 7.5 \pm 0.7 | | |
| <i>M. junakii</i> | 8.6-10 | 3.5-5.5 | 5-6 | 1.4-2 | 5.5-6.2 | | |
| N = 31 | 9.0 \pm 0.8 | 3.8 \pm 0.7 | 5.3 \pm 0.5 | 1.8 \pm 0.2 | 5.4 \pm 0.4 | | |
| <i>M. foliosa</i> ssp. <i>philbrickii</i> | 8.3-15.2 | 3.5-7.3 | 5-10.8 | 2-4 | 5.1-8.2 | | |
| N = 39 | 10.7 \pm 0.8 | 5.1 \pm 0.7 | 7.1 \pm 0.7 | 3.2 \pm 0.4 | 6.2 \pm 0.5 | | |
| <i>M. foliosa</i> ssp. <i>polyccephala</i> | 5.3-8.5 | 2.5-4 | 3-5.5 | 1.5-2.7 | 2.9-5 | | |
| N = 45 | 7.4 \pm 1.0 | 2.9 \pm 0.6 | 4.7 \pm 0.7 | 3.1 \pm 0.5 | 4.1 \pm 0.6 | | |
| <i>M. squilida</i> | 12-18.5 | 5.8-10.5 | 8-13 | 2-3 | 6.2-9.5 | | |
| N = 37 | 16.2 \pm 1.6 | 8.1 \pm 1.3 | 10.8 \pm 1.2 | 2.6 \pm 0.2 | 7.8 \pm 0.7 | | |

TABLE 3. PERCENTAGE OF STAINABLE POLLEN IN F_1 HYBRIDS BETWEEN MEMBERS OF THE *M. FOLIOSA* COMPLEX. COU = *M. coulteri*, JUN = *M. junakii*, SQU = *M. squalida*, FOL/PHI = both *M. foliosa* ssp. *foliosa* and *M. f.* ssp. *philbrickii* as parents (given are range, mean \pm standard deviation, and number of hybrids analysed, N).

| | COU | JUN | SQU | FOL/PHI |
|---------|-----------------------------------|-------------------------------------|------------------------------------|------------------------------------|
| COU | 75-98 92.4 \pm 8.3 N = 8 | | | |
| JUN | 5-28 12.28 \pm 7.6 N = 7 | 46-100 91.0 \pm 17.3 N = 22 | | |
| SQU | 0-42 22.7 \pm 13.9 N = 16 | 10-32 18.3 \pm 7.0 N = 20 | 55-100 96.5 \pm 9.8 N = 12 | |
| FOL/PHI | 0-40 12.5 \pm 10.9 N = 17 | 2-58 28.4 \pm 17.1 N = 14 | 12-58 31.4 \pm 14.4 N = 20 | 85-100 97.8 \pm 1.5 N = 62 |

Santa Barbara (PHI), West Anacapa (CRI), and East Anacapa (CRI). Islands where two taxa of the *M. foliosa* complex occur are Middle Anacapa (JUN and SQU), San Miguel (INC and IND), San Nicolas (INC and POL), Santa Cruz (IND and SQU), and Santa Rosa (INC and IND). Both FOL and INS have been collected on the south islet of Los Coronados Island, but the former has not been seen there since 1926, and the few available herbarium specimens of FOL and INS from the island provide no evidence of hybridization. As far as is known, different diploid taxa of the *M. foliosa* complex are not sympatric except on San Miguel Island and San Nicolas Island. In the latter case, INC is a recent addition to the flora and is freely hybridizing with the annual POL (Davis and Junak 1988). This case of natural hybridization between two of the most different diploid taxa of the *M. foliosa* complex is consistent with evidence from growth chamber studies that there is a general lack of biological isolating mechanisms between diploid members of the group, excluding COU. On San Miguel Island, putative hybrids between INC and IND recently have been found, but the situation has not yet been analyzed.

DISCUSSION

This study indicates that six of the diploid members of the *M. foliosa* complex (*Malacothrix foliosa* ssp. *crispifolia*, *M. f.* ssp. *foliosa*, *M. f.* ssp. *philbrickii*, *M. f.* ssp. *polycephala*, *M. incana*, and *M. indecora*, but not *M. coulteri*) are essentially interfertile, and constitute a closely knit group, both morphologically and biogeographically. Morphological differentiation in the group has occurred more rapidly than development of reproductive isolating mecha-

nisms between taxa. This, together with current insular distributions and patterns of morphological differentiation, suggests that adaptive radiation has been involved in the origin of at least some taxa.

In a future report more detailed evidence will be presented to support particular relationships within the *M. foliosa* complex, and specific hypotheses concerning the origins of all of the taxa. However, the hypothesis that self-compatible, self-pollinating *M. f. ssp. polycephala* has been derived from *M. f. ssp. foliosa* is particularly well-supported by morphological, physiological, and biogeographical evidence, and will be briefly discussed here. The two taxa are similar with respect to growth habit, growth rate in cultivation, cauline leaf morphology, involucre structure, achene micromorphology, and habitat preference, but differ consistently with respect to the size of several quantitative floral traits (Table 2). In addition, current island distributions and breeding system evidence from growth chamber studies lend support to the hypothesis that *M. f. ssp. foliosa* was the progenitor and *M. f. ssp. polycephala* the derivative in a process of adaptive radiation that involved dispersal of self-compatible plants of *M. f. ssp. foliosa* from San Clemente Island to San Nicolas Island, fixation of self-compatibility, and selection for reduction in size of floral traits.

In addition, morphological, biogeographical, and chromosomal evidence from this study suggests that the polyploid *M. squalida* is an amphidiploid between *M. foliosa* ssp. *philbrickii* and *M. coulteri*. Artificial hybrids between the putative parents are sterile (Table 3), and generally indistinguishable from *M. squalida* in critical diagnostic traits. Triploid hybrids between *M. squalida* and *M. coulteri* or *M. foliosa* ssp. *foliosa* have reduced pollen stainability, and the maximum chromosome association found at diplonema of meiosis is 7 pairs and 7 univalents. The current and past distributions of the taxa also are consistent with the hypothesis.

TAXONOMY

Following is a key to the annual taxa of *Malacothrix* endemic to the California Islands.

1. Corollas generally <10 mm long; ligules of outermost florets exerted <4 mm beyond the involucre
2. Plants generally mat-like, 2–10 cm tall, branched from the base; cauline leaves generally fleshy, margins with 3–8 pairs of short, obtuse, nearly equal lobes; tips of outer phyllaries obtuse (2) *M. indecora*
- 2' Plants not mat-like, generally 10–30 cm tall, branched from the base or above; cauline leaves not generally fleshy, margins toothed or with narrow, sharp lobes; tips of outer phyllaries acute or broadly acute
3. Margins of cauline leaves crisped; longest outer phyllaries nearly as long as inner phyllaries; fruit 1.4–1.6 mm long, 15-ribbed and 5-angled; endemic to Anacapa Island (1a) *M. foliosa* ssp. *crispifolia*
- 3' Margins of cauline leaves not crisped; longest outer phyllaries generally ca.

- half as long as inner phyllaries; fruit 0.9–1.3 mm long, evenly 15-ribbed; endemic to San Nicolas Island (1d) *M. foliosa* ssp. *polycephala*
- 1' Corollas generally >10 mm long; ligules of outermost florets generally exerted >5 mm beyond the involucre
4. Outer phyllaries 20–26, hyaline/scarios margins >0.5 mm wide
5. Fruit with 1–3 smooth, persistent setae; tips of 5 strongest ribs generally not extended above the tips of lesser ribs at achene apex; endemic to Los Coronados Island (3) *M. insularis*
- 5' Fruit generally without persistent setae; tips of 5 strongest ribs extended beyond the tips of lesser ribs at the achene apex; endemic to Middle Anacapa and Santa Cruz islands (5) *M. squalida*
- 4' Outer phyllaries 9–19, hyaline/scarios margins <0.4 mm wide
6. Fruit without an outer pappus; plants diploid, >70% of stainable pollen 3-pored
7. Stems usually one from a tap-root, branched above, erect; uppermost cauline leaves with 1–3 pairs of long, narrow lobes at the base, the distal $\frac{2}{3}$ with entire margins; achene 15-ribbed, ribs generally equal; endemic to San Clemente and Los Coronados islands (1b) *M. foliosa* ssp. *foliosa*
- 7' Stems one, or more often several from a taproot, branched above, decumbent to erect; margins of uppermost cauline leaves generally evenly toothed or lobed nearly to the apex; fruit 15-ribbed and 5-angled; endemic to Santa Barbara Island (1c) *M. foliosa* ssp. *philbrickii*
- 6' Fruit with an outer pappus of minute teeth and 1 naked persistent seta; tetraploid ($2n = 28$), >70% of stainable pollen 4-pored; endemic to middle Anacapa Island (4) *M. junakii*

1. *Malacothrix foliosa* A. Gray, Synoptical Flora of North America edition 2. 12:455. 1886.—Type: USA, California, Los Angeles Co., San Clemente Island, April 1885, *Nevin and Lyon s.n.* (holotype: GH!; isotypes: CAS!, DS!, UC!).

Plants annual from a taproot, 5–50 cm tall. Stems one to several from the base, branched above, decumbent, ascending, or erect, pale green to medium red, essentially glabrous, but arachnoid at leaf axiles. Basal leaves 5–14 cm long, 6–40 mm wide, oblanceolate to narrowly obovate, margins toothed or pinnately lobed or divided, tips broadly acute to attenuate acute; lower cauline leaves like basal leaves but more deeply lobed or divided; uppermost cauline leaves pinnately lobed or divided, tips acute to attenuate acute. Heads 2–7 mm wide at anthesis, base tapered or rounded. Involucre 5–12 mm high; outer phyllaries 7–20, lanceolate to narrowly ovate, 1.5–6.4 mm long, 0.7–2 mm wide, nearly as long or noticeably shorter than the inner pappus, tips acute to broadly acute, green, red-tinged, or red, the midvein and tips generally darker red, hyaline/scarios margins <0.3 mm wide; inner phyllaries 8–22, linear-lanceolate, 5–8 mm long, 0.8–2 mm wide, generally pale to medium green or red-tinged, hyaline/scarios margins <0.3 mm. Receptacle naked. Florets 15–120; corolla 5–17 mm long, light yellow to medium yellow, ligules of outermost florets 2–3 mm wide, exerted 1.5–10 mm beyond the involucre. Stamens 3–8.2 mm long; style branches 0.2–0.7

mm long, fruit 0.9–1.6 mm long, cylindric-fusiform, the base narrower than the constricted, truncate apex, brown to dark brown, equally 15-ribbed, or 5-angled; outer pappus none (very rarely one or two naked, weakly persistent setae). Self-compatible or self-incompatible. $2n=14$.

- 1a. **Malacothrix foliosa** A. Gray ssp. **crispifolia** W. S. Davis ssp. nov.—TYPE: USA, California, Ventura Co., Anacapa Island, east island, grassy northeast-facing slope, east of Lighthouse, 22–23 April 1970, *Benedict s.n.* (holotype: SBBG!; isotype: SBBG!).

Plantae annuae, 8–20 cm altae. Caulis unicus vel e basi aliquot, supra ramosus, ascendens vel arrectus. Folia caulina superna oblanceolata vel ovato-obovata in apice acuta in superficie abaxiali in areis parvis tomentosa in marginibus pinnatim in 2–5 segmenta angusta dentata attenuato-acuta crispata divisa, basin versus interdum integra vel solummodo dentata; folia suprema oblanceolata in marginibus usque regionem apicalem pinnatim brevi-lobata. Capitula sub anthesi 3.4–5.4 mm lata in base plerumque rotundata. Involucrum 7–9.2 mm altum; phyllaria exteriora 10–20, quam phyllaria interiora aliquantum breviora pallido- vel atro-rubra plerumque in apice atriora; phyllaria interior 12–20, viridia vel pallide rubra. Flosculi 20–80; corollae 6–10 mm longae mediocriter flavae; ligulae flosculorum extimorum 2.1–2.7 mm latae, trans involucrum 2.5–4 mm exsertae; stamina 4.3–6 mm longa; ramuli styli 0.2–0.4 mm longi. Fructus 1.3–1.6 mm longus, leniter 5-angulus, uniformiter atro-fuscus. Autogamae et aptae se pollinare.

Plants annual, 8–20 cm tall. Stems one to several from the base, branched above, ascending to erect, pale red to deep red. Upper cauline leaves oblanceolate to ovate-obovate, apically acute, abaxial surface tomentose in patches, margins pinnately parted into 2–5 narrow, toothed, attenuate-acute, crisped segments, basally sometimes entire or only toothed; uppermost leaves oblanceolate, margins pinnately short lobed to near the apex. Heads 3.4–5.4 mm wide at anthesis, base generally rounded. Involucre 7–9.2 mm high; outer phyllaries 10–20, nearly as long as inner phyllaries, pale red to dark red, tips generally darker; inner phyllaries 12–20, green to pale red. Florets 20–80; corollas 6–10 mm long, medium yellow; ligules of outermost florets 2.1–2.7 mm wide, exserted 2.5–4 mm beyond involucre; stamens 4.3–6 mm long; style branches 0.2–0.4 mm long. Fruit 1.3–1.6 mm long, somewhat 5-angled, evenly dark brown. Self-compatible and self-pollinating.

Paratypes (* progenies from wild achenes propagated in growth chambers). USA, California: Ventura Co., Anacapa Island, east island, east portion, n-facing slope, e of Lighthouse, 22–23 April

1970, *Benedict s.n.* (SBBG); east island, 25 April 1959, *Blakley 277* (SBBG); west island, n slope of hill between Frenchman's Cove and e end, 31 March 1962, *Blakley 4940* (SBBG, DHL); east island, rare on flats just north of road between Ranger's residence and lighthouse, 23 August 1978, *Junak and Hochberg s.n.* (SBBG)*; west island near Frenchies Cove, 5 June 1962, *Davis 171* (DHL)*; west island, near ridge on steep slope above landing, north side (Frenchman's Cove), 70 ft, 11 May 1963, *Piehl 63268* (DHL, SBBG).

Only self-compatible plants were found in progenies from wild seed, and from intrataxon crosses. A majority of the plants were also strongly self-pollinating (mean percentage of filled/pigmented achenes from undisturbed heads 70%).

1b. *Malacothrix foliosa* A. Gray ssp. *foliosa*

Plants annual, 4–45 cm tall. Stems generally one from the base, generally erect, glabrous, pale-green to red-tinged. Uppermost cauline leaves ovate to lanceolate, pinnately parted at the base into 1–2 long, narrow segments, margins of the distal $\frac{2}{3}$ entire. Heads 3.1–6.7 mm wide at anthesis, base tapered. Involucre 7–11 mm high; outer phyllaries 9–19, generally half the length of inner phyllaries, reddish green, tips dark red; inner phyllaries 13–22, pale green to reddish. Florets 50–120; corollas 10–17 mm long, light yellow; ligules of outermost florets 2–4 mm wide, exserted 5–10 mm beyond the involucre; stamens 5.3–8.1 mm long; style branches 0.3–0.7 mm long. Fruit 0.9–1.5 mm long, medium to dark brown, generally evenly 15-ribbed. Self-compatible or self-incompatible.

Representative specimens (* progenies from wild achenes propagated in growth chambers). USA, California, Los Angeles Co., San Clemente Island, vicinity of Mosquito Harbor, 6 July 1931, *Abrams and Wiggins 339* (CAS, DS, GH, UC); on a north slope, China Point, 9 June 1962, *Blakley 5191* (CAS, SBBG); Wilson Cove, 10 June 1962, *Blakley 5220* (CAS SBBG)*; Wilson Cove, above and n of Seal Cove, 10 June 1962, *Blakley 5234* (SBBG); sand dune area, nw side of island, 15 May 1985, *Davis 457* (DHL)*; along road to Eel Point, 15 May 1985, *Davis 458* (DHL)*; slopes above Eel Point, 15 May 1985, *Davis 459* (DHL)*; southeast point, 2 April 1939, *Dunkle 7211* (DS, LAM, SBBG, UNM); Camp Mesquite, 4 July 1919, *Knoche 982* (DS); sandy beach due west of Wall 2, 11 April 1962, *Raven 17279* (CAS, DS, SBBG, SD, RSA, UC)*; second canyon s of Seal Cove, 8 May 1962, *Raven 17606* (RSA)*; Wilson Cove, 11 April 1962, *Raven 17291* (RSA, UC)*; Wilson Cove, 8 May 1962, *Raven 17625* (RSA, SBBG, SD, UC)*; e end of Northwest Harbor, 100 ft, 12 July 1962, *Raven 18026* (RSA)*; n of Eel Point, *Ross 5442* (SBBG)*; west cove, sw of new landing field, *Ross 5080* (SBBG)*; China Point, 12 April 1973, *Thorne*

42908 (RSA); dunes near Flasher, nw part of island, 10–15 ft, 11 April 1973, *Thorne 42879* (CAS, TEX)*; north end, east coast, 9 April 1923, *Munz 6612* (POM, UC). MEXICO: Baja California Norte. Los Islas Coronados, 12 May 1895, *A. W. Anthony s.n.* (UC); 10 June 1926, *M. E. Jones s.n.* (POM); 30 May 1926, *W. M. Pierce s.n.* (POM, specimen on the left).

In cultivation, 19% of the plants grown from wild achenes were self-incompatible. Self-compatible plants were poorly self-pollinating (<40% of the achenes were filled/pigmented in undisturbed heads. *Malacothrix foliosa* was collected on Los Coronados Island in the past, but not since 1926.

- 1c. ***Malacothrix foliosa*** A. Gray ssp. ***philbrickii*** W. S. Davis ssp. nov.—TYPE: USA, California, Santa Barbara Co., Santa Barbara Island, west side, 100 m, 27 April 1941, *Moran 824* (holotype: DS!; isotypes: CAS!, UC!, US!).

Plantae annuae, 6–35 mm altae. Caulis unicus vel e basi aliquot, supra ramosus decumbens ascenden vel arrectus. Folia superna caulina ovato-obovata vel lanceolato-oblancheolata, in marginibus vel dentata, longi-serrata vel pinnatim lobata vel in 2–4 paria segmentorum dentatorum plerumque non crispatorum divisa; folia supremus lanceolato-oblancheolata, apicem versus acuta vel obtusa, in marginibus dentata vel apicem versus brevi-lobata. Capitula sub anthesi 3.1–6.7 mm lata, in base subcontacta. Involucrum 7–11 mm altum; phyllaria exteriora 9–19, phyllariis interioribus 2plo vel aliquantum breviora, pallide viridia vel rubrescenti-viridia, in apice subatriora et squarrosa; phyllaria interiora 11–21, subviridia vel viridia. Flosculi 40–113; corollae 8–16 mm longae, mediocriter flavae; ligulae flosculorum extimorum 2–4 mm latae trans involucrum 4–8 mm exsertae; stamina 5–8 mm longa; ramuli styli 0.4–0.7 mm longi. Fructus 1.3–1.7 mm longus, mediocriter vel atro-fuscae, plerumque 5-angulus. Autogamae vel non autogamae.

Plants annual, 6–35 cm tall. Stems one to several from the base, branched above, decumbent, ascending to erect. Upper cauline leaves ovate-obovate to lanceolate-oblancheolate, margins dentate, long-serrate, or pinnately lobed or parted into 2–4 pairs of toothed, generally not crisped segments; uppermost leaves lanceolate-oblancheolate, apically acute to obtuse, margins toothed or short lobed to near the tip. Heads 3.1–6.7 mm wide at anthesis, base somewhat tapered. Involucre 7–11 mm high; outer phyllaries 9–19, ½ as long to nearly as long as inner phyllaries, pale green to reddish green, tips generally darker, and squarrose; inner phyllaries 11–21, pale green to green. Florets 40–113; corollas 8–16 mm long, medium yellow; ligules of outermost florets 2–4 mm wide, exserted 4–8 mm beyond involucre; stamens 5–8 long; style branches 0.4–0.7 mm

long. Fruit 1.3–1.7 mm long, medium to dark brown, generally 5-angled. Self-compatible or self-incompatible.

Paratypes (* progenies from wild achenes propagated in growth chambers). USA, California: Santa Barbara Co., Santa Barbara Island, Cliff Canyon, 5 May 1963, *Blakley 5696* (SBBG, RSA); bluff, due w of mouth of Cliff Canyon, 200 ft, 21 May 1966, *Philbrick and Benedict B66–373* (SBBG)*; bluff, halfway between Landing Cove & Cliff Canyon, 21 May 1966, *Philbrick and Benedict B66–371* (SBBG)*; canyon between Landing Cover and Cliff Canyon, 18 March 1968, *Philbrick B68–32* (CAS, SBBG); lower Middle Canyon, 22 March 1970, *Philbrick and Benedict 70–53* (SBBG); upper part of Graveyard Canyon, 27 April 1968, *Thorne 37512* (RSA); 3 July 1931, *Abrams and Wiggins 304* (DS, UC); above landing, along steps leading to Ranger's Residence, 3 July 1982, *Davis 434* (DHL)*; cliffs above Graveyard Canyon, 3 July 1982, *Davis 435* (DHL)*; upper southern margins of Middle Canyon, 3 July 1982, *Davis 436* (DHL)*; dry ridge along trail n of Ranger's Residence, 3 July 1982, *Davis 437* (DHL)*; along trail s of Middle Cliff Canyon, 3 July 1982, *Davis 438* (DHL)*; along path through desert pavement area, nw tip of island, 3 July 1982, *Davis 439* (DHL)*; west side, common, 28 May 1939, *M.B. Dunkle 8133* (DS, LAM, SBBG, UNM); just above landing platform, Landing Cove, 21 May 1966, *Philbrick and Benedict B66–356* (SBBG); east side of embayment of Cat Canyon, 28 April 1968, *Thorne 37485* (CAS, DS, RSA); north slope of Signal Peak, 4 May 1963, *Blakley 5677* (SBBG).

PHI is particularly variable in growth habit and cauline leaf morphology, and at least two distinct ecotypes are recognizable. On the windy northwest side of Santa Barbara Island, on open flats with coarse, gravelly soil, is a low-growing decumbent form with 5–10 abundantly leafy stems from the base. On the drier southeast side, in among shrubs and other vegetation in small canyons or draws, is an erect form, generally with a single stem from the base and branched above, with cauline leaves reduced upward. The two ecotypes breed true in cultivation and are indistinguishable in floral morphology.

Thirty-one percent of the plants of PHI grown in cultivation from wild achenes were self-incompatible. Self-compatible plants were poorly self-pollinating (<10% of the achenes from mature undisturbed heads were pigmented/filled).

- 1d. ***Malacothrix foliosa* ssp. *polycephala*** W. S. Davis ssp. nov.—
TYPE: USA, California, Ventura Co., San Nicolas Island, annual, pale yellow flowers, clay slopes about 200–300 ft elevation, above the docks scattered near the west end of the island;

colonial San Nicolas Island, 24 April 1966, *Raven and Thompson 20784* (holotype: MO; isotypes: CAS!, DHL!, DS!, JEPS!, NY, OBI!, SBBG!, UC!, US!).

Plantae annuae, 10–35 mm altae. Caulis plerumque e basi unicus, supra ramosus, ascendens vel arrectus, pallide vel mediocriter ruber. Folia superna caulina ovata, in marginibus pinnatim in 3–4 segmenta angusta plerumque dentata non crispata divisa; folia suprema triangularia, basem versus in 1–2 paria segmentorum longorum angustorum divisa, in marginibus partis $\frac{2}{3}$ distalis integra. Capitula sub anthesi diametro 2–4.5 mm, in base subcontracta. Involucrum 5–7 mm altum; phyllaria exteriora 7–15, plerumque phyllariis interioribus longitudine 2plo breviora, rubra in apice et atriora; phyllaria interiora 8–14 subrubra. Flosculi 15–17; corollae 5.3–9 mm longae mediocriter flavae; ligulae flosculorum extimorum 1.5–3.3 mm latae, trans involucrum 1.5–3.5 mm exsertae; stamina 2.9–5 mm longa; ramuli styli 0.4–0.5 mm longi. Fructus 0.9–1.3 mm longus mediocriter vel atrofuscae plerumque aequaliter 15-costatus. Autogamae et aptae se pollinare.

Plants annual, 10–35 cm tall. Stems generally solitary from the base, branched above, ascending to erect, pale red to medium red. Upper cauline leaves ovate, margins pinnately parted into 3–4 narrow, often toothed, not crisped segments; uppermost leaves triangular, parted near the base into 1–2 pairs of long narrow segments, margins of distal $\frac{2}{3}$ entire. Heads 2–4.5 mm wide at anthesis, base somewhat tapered. Involucre 5–7 mm high; outer phyllaries 7–15, generally $\frac{1}{2}$ the length of the inner, red with darker red tips; inner phyllaries 8–14, reddish. Florets 15–70; corolla 5.3–9 mm long, medium yellow; ligules of outermost florets 1.5–3 mm wide, exserted 1.5–3.5 mm beyond the involucre; stamens 2.9–5 mm long; style branches 0.4–0.5 mm long. Fruit 0.9–1.3 mm long, medium to dark brown, generally evenly 15-ribbed. Self-compatible and self-pollinating.

Paratypes (* progenies from wild achenes propagated in growth chambers). USA, California: Ventura Co., San Nicolas Island, flats above ravine area between Tranquility Beach and Corral Harbor, 30 May 1986, *Davis 468* (DHL)*; above Tranquility Beach near NAVFAC, 30 May 1986, *Davis 469* (DHL)*; along Tufts Road, 30 May 1986, *Davis 470* (DHL)*; near triangulation point east of Tule Creek, 11 June 1969, *Philbrick and Benedict B69-184* (SBBG); west Jehemy Beach, 10 June 1969, *Philbrick and Benedict B69-171* (SBBG); mesa, between Celery Creek and pond, 10 June 1969, *Philbrick and Benedict B69-135* (SBBG); between Elephant Seal and Dutch Harbor, 24 April 1966, *Raven and Thompson 20784* (DHL, CAS, etc.); near w end of island, 24 April 1966, *Raven and Thompson* (DHL, etc.)*; Sewage Canyon, 12 March 1977, *Smith s.n.*

(DHL)*; near center of the island, 13 March 1977, *Smith s.n.* (DHL)*; near mouth of Celery Canyon, 28 July 1965, *Forman 80* (US); west of Tule Canyon, 4 July 1978, *Wier and Beauchamp s.n.* (UC); area on the ridge, April 1897, *Trask 108* (MO, UC, US).

Only self-compatible plants were found in progenies from wild seed or from intrataxon crosses. A majority of plants were strongly self-pollinating (>70% of the achenes in undisturbed heads were pigmented/filled).

Because of natural hybridization between INC and POL, it is becoming difficult to distinguish between pure POL and hybrid plants in some areas on San Nicolas Island, particularly on the north-west or west sides adjacent to the ocean.

2. *Malacothrix indecora* Greene. Bulletin of the California Academy. 2:152. 1886.—*Malacothrix foliosa* var. *indecora* E. Williams, American Midland Naturalist 58:507.—TYPE: USA, California, Santa Barbara Co., Santa Cruz Island, July and August 1886, *E. L. Greene s.n.* (holotype: CAS!; isotypes: DS!, GH!, MO!, ND-G!, NY!, UC!, US!).

Plants annual, 2–15 cm tall, generally mat-like. Stems several from the base, branched above, green to pale red, essentially glabrous, arachnoid in leaf axiles. Basal leaves obovate, 2–5 cm long, 0.5–1 mm wide, somewhat fleshy, obtusely 4–8-lobed. Cauline leaves similar to basal leaves but somewhat reduced upward. Heads 2–7 mm wide at anthesis, base rounded. Involucre 6–8 mm high; outer phyllaries 22–32, generally ovate, nearly as long as the inner, 1.1–4.2 mm long, 0.4–1.7 mm wide, green to red-tinged, slightly constricted below the obtuse tip, hyaline/scarious margins <0.3 mm wide; inner phyllaries 19–23, linear-lanceolate, 5.2–7.2 mm long, 1–1.8 mm wide, green, tips of alternate ones often paler green, hyaline/scarious margins <0.3 mm wide. Florets 22–81; corolla 4–8 mm long, greenish yellow; ligules of outermost florets 1.5–2.5 mm wide, exserted 1.3–3.3 mm beyond the involucre; stamens 3.4–5.4 mm long; style branches 0.2–0.5 mm long. Fruit 1.2–1.6 mm long, narrowed at the base, the apex truncate and slightly constricted, dark brown, 15-ribbed and 5-angled; outer pappus none. Self-compatible, and self-pollinating. $2n=14$.

Representative specimens (* progenies from wild achenes propagated in growth chambers). USA, California: Santa Barbara Co., San Miguel Island, Twin Harbor on indian mound, 18 July 1939, *Williams 87* (POM); mesa above sea, 19 April 1932, *Hoffmann 692* (UC); n of mouth of Willows Canyon, 19 April 1932, *Hoffmann 694* (UC, LL); rocky knoll opposite Prince's Island, 19 April 1932, *Hoffmann s.n.* (SBBG); seaward edge of coastal flats just n of mouth of Willow Canyon, ca. 50 ft, 20 July 1995, *Junak and Williams*

6061 (SBBG)*; rocky bench just e of Cuyler Harbor, s of e end of Prince Island, ca. 20 ft, 20 July 1995, *Junak and Williams 6057* (SBBG)*. Santa Cruz Island, Black Point, 9 March 1980, *Junak SC-262* (DHL, SBBG)*; Black Point, 19 June 1980, *Junak SC-312* (SBBG)*. Santa Rosa Island, bluff on w side of mouth of Canada Lobos, 10 m, *D. H. Wilken 15219* (SBBG, DHL).

All of the plants grown in cultivation were self-compatible, but poorly to moderately self-pollinating (10–50% filled/pigmented achenes in undisturbed heads). On Santa Cruz Island *M. indecora* is restricted to soils derived from metamorphic and igneous rocks (Junak et al. 1995), and on San Miguel Island it is restricted to coastal flats on soils derived from igneous rocks.

3. *Malacothrix insularis* E. L. Greene, Bulletin of the California Academy of Sciences. 1:194. 1985.—TYPE: MEXICO, Baja California Norte, Coronados Island, May 16, 1885, *Edward L. Greene s.n.* (holotype: CAS!; isotypes: CAS!, DS!, UC!, US!).

Plants annual, 10–45 cm tall. Stems one, or less often several from the base, branched above, ascending or erect. Basal leaves lanceolate-ob lanceolate, 5–12 cm long, 10–25 mm wide, divided-pinnatifid, the lobes narrowly triangular with entire margins, and apically acute; cauline leaves lanceolate to narrowly ovate, reduced upward, the basal $\frac{1}{2}$ pinnately 1–3 parted into narrow, attenuate acute segments, the distal $\frac{1}{2}$ with entire margins. Heads 7–10 mm wide at anthesis, base rounded. Involucre 10–12 mm high; outer phyllaries 20–27, broadly lanceolate to ovate, or spatulate, 3–5 mm long, 2–2.5 mm wide, the midvein generally dark red, hyaline/scarious margins 0.5–1.0 mm wide; inner phyllaries 20–25, linear-lanceolate, 6–8 mm long, 1–1.5 mm wide, hyaline/scarious margins 0.3–0.5 mm wide, central midvein generally dark red; receptacle with thin, short, naked bristles <1.4 mm long; florets 35–160; corollas 10–15 mm long, yellow; ligules of outermost florets 2–2.5 mm wide, exerted 4–6 mm beyond the involucre; stamens 6–9 mm long; style branches 0.6–1.1 mm long. Fruit 2.0–2.6 mm long, the apex slightly constricted, 15-ribbed with 5 ribs more prominent than the others, but the apices not extended beyond lesser ribs at the apex, brown to tan in color; outer pappus a ring of scarious, triangular or needle-like teeth interspersed with 1–3 unbarbed persistent bristles to 5 mm long. $2n$ = unknown.

Specimens examined. MEXICO, Baja California Norte: Los Coronados Island, 30 May 1926, *W.M. Pierce s.n.* (POM, specimen on the right); west slope in southern part of South Island, 8 May 1976, *Moran 23158* (RSA, SD, SBBG).

Living material of INS was not available, but pollen stainability

of herbarium specimens was 70–100%. Pollen was 4–6-pored, and modally larger in diameter than the pollen of either of the two known polyploids (SQU and JUN). It is likely, therefore that INS is polyploid. The most recent collection, by Reid Moran in 1976, reported a single colony of about 100 individuals on steep west slopes in the southern part of the south islet (listed in field notes as *M. coulteri*).

4. ***Malacothrix junakii*** W. S. Davis sp. nov.—TYPE: USA, California, Ventura Co., Anacapa Island, middle island, west-facing slope with *Coreopsis gigantea*, *Eriogonum grande*, extreme tip of Sea Arch Peninsula, distal from Arch, 2 June 1978, *Philbrick B78-327* (holotype: SBBG!, top left specimen; isotype: DHL!).

Plantae annuae, 5–30 cm altae. Caulis unicus vel aliquot e radice palari oriens, supra ramosus, ascendens vel arrectus, viridis vel mediocriter ruber, glaber. Folia basalia 4–10 cm longa, 5–20 mm lata, oblanceolata, in dimidio distali dentibus 2–3 vel lobis pinnatis 2–4 in segmenta brevia obtusa divisio instructa. Folia caulina late lineari-lanceolata, pinnatim 2–4-lobata, lobis angustis et longitudine subaequalibus praedita; folia superna in base in 1–2 segmenta angusta acuta pinnatim divisa, in marginibus partis $\frac{2}{3}$ distalis integra. Capitula sub anthesi 3–6 mm lata, in base rotundata; involucrum 7–8.5 mm altum; phyllaria exteriora 7–11, lanceolata vel ovata, 1.2–3.5 mm longa, 1–1.5 mm lata, plerumque phyllariis interioribus 2plo breviora, viridia vel rubro-tincta, marginibus hyalinis scariosis <0.3 mm latis instructa; phyllaria interiora 9–13, lineari-lanceolata, 5–7 mm longa, 1–1.6 mm lata, acuta. Receptaculum setis paucis gracilibus nudis <0.6 mm longis armatum. Flosculi 20–85; corollae 7–11 mm longae mediocriter flavae; ligulae flosculorum extimorum 1.4–2 mm latae, trans involucrum 3.5–5.5 mm exsertae; stamina 5–6.2 mm longa; ramuli styli 0.4–0.7 mm longi. Fructus 1.6–2 mm longus, cylindrico-fusiformis, in base angustior quam in apice subconstricto truncato, plerumque atro-fuscus, aequaliter 15-costatus vel leniter 5-angulus; pappus exterior dentibus perbrevis irregularibus armatus e setis 1–2 persistentibus nudis usque 4 mm longis compositus. Autogamae.

Plants annual, 5–30 cm tall. Stems one to several from a taproot, branched above, ascending to erect, green to medium red, glabrous. Basal leaves 4–10 cm long, 5–20 mm wide, oblanceolate, distal $\frac{1}{2}$ with 2–3 teeth, or pinnately 2–4-lobed with short, obtuse segments. Cauline leaves broadly linear-lanceolate, pinnately 2–4-lobed, lobes narrow and approximately equal in length; uppermost leaves pinnately 1–2-parted at the base into narrow, sharp segments, margins of the distal $\frac{2}{3}$ entire. Heads 3–6 mm wide at anthesis, base rounded; involucre 7–8.5 mm high; outer phyllaries 7–11, lanceolate to ovate, 1.2–3.5 mm long, 1–1.5 mm wide, generally $\frac{1}{2}$ as long as inner

phyllaries, green to red-tinged, hyaline scarious margin <0.3 mm; inner phyllaries 9–13, linear-lanceolate, 5–7 mm long, 1–1.6 mm wide, acute. Receptacle with few thin, naked bristles <0.6 mm long. Florets 20–85; corollas 7–11 mm long, medium yellow; ligules of outermost florets 1.4–2 mm wide, exerted 3.5–5.5 mm beyond the involucre; stamens 5–6.2 mm long; style branches 0.4–0.7 mm long. Fruit 1.6–2 mm long, the base narrower than the slightly constricted truncate apex, generally dark brown, equally 15-ribbed or somewhat 5-angled; outer pappus of very short irregular teeth and 1–2 persistent naked setae to 4 mm long. Self-compatible. $2n=28$.

Paratypes (* progenies from wild achenes propagated in growth chambers). USA, California: Ventura Co., Anacapa Island, moist sheltered pocket, 19 May 1928, *Howell 3795* (CAS); middle island, Lavatera Cove, ca. 75 ft, 23 April 1982, *Junak MA-60* (SBBG)*; middle island, slopes above East Fish Camp, on east edge of major gully running down to shoreline, south side of island, rare on open south-facing slope, 80 ft, 29 April 1986, *Junak MA-145* (DHL, SBBG)*; middle island, onshore slope, at foot of Sea Arch Peninsula, west of Sheep Camp, localized on flats and adjacent coastal bluffs, 80 ft, 22 April 1986, *Junak MA-105* (DHL, SBBG)*.

5. *Malacothrix squalida* Greene, Bulletin of the California Academy of Sciences 2:152. 1886.—*Malacothrix foliosa* var. *squalida* E. Williams, American Midland Naturalist 58:507. 1957.—*Malacothrix insularis* var. *squalida* Ferris, Contributions from the Dudley Herbarium 5:102. 1958.—TYPE: USA, California, Santa Barbara Co., rocky promontory above Prisoner's Harbor, Santa Cruz Island, July and August 1886, *E.L. Greene s.n.* (holotype: CAS!; isotypes: DS!, ND-G!, NY!, UC!).

Plants annual from a taproot, 4–30 cm tall. Stems generally several from the base. Basal leaves oblanceolate, 4–14 cm long, 10–25 mm wide, with teeth or narrow, toothed sharp lobes. Lower cauline leaves similar to basal leaves but more deeply toothed or lobed; upper cauline leaves ovate to narrowly triangular, with 4–9 narrow, sharp, generally toothed lobes. Heads 6–10 mm wide at anthesis, base rounded. Involucre 9–12 mm high; outer phyllaries 12–26, ovate to broadly ovate, 2.5–7 mm long, 1.8–2.5 mm wide, with dark mid-veins, hyaline/scarious margins 0.5–1 mm wide and irregularly toothed; inner phyllaries 19–23, linear-lanceolate 6–9 mm long, 1.6–2.5 mm wide, green or reddish, hyaline/scarious margins <0.4 mm wide. Receptacle with scattered naked bristles 0.1–0.5 mm long. Florets 30–160; corollas 12–19 mm long, light yellow; ligules of outermost florets 2–3 mm wide, exerted 6–10.5 mm beyond the involucre; stamens 6–9.5 mm long; style branches 0.5–0.7 mm long. Fruit 1.5–2.2 mm long, medium to dark brown, 15-ribbed, 5-angled,

tips of more prominent ribs extended above the lesser ribs at the achene apex; outer pappus of irregular teeth, and no persistent setae (rarely 1). Self-compatible. $2n=28$.

Specimens examined (* progenies propagated from wild achenes in growth chambers). USA, California: Ventura Co., Middle Anacapa Island, at e end of knife edge area, 1 June 1978, *Philbrick and Hochberg* B78-288 (SBBG)*; e of knife edge mesa near triangulation point, 12 May 1968, *Piehl* 63290 (SBBG); n end of island, 2 July 1931, *Abrams and Wiggins* 270 (UC). Santa Barbara Co., Santa Cruz Island. E-facing slope, canyon draining from Coche Point to Potato Harbor, 8 May 1968, *Philbrick, Mcpherson, and Benedict* B68-292 (SBBG); 1888, *T. S. Brandege* s.n. (UC).

All of the plants grown in cultivation were self-compatible and strongly self-pollinating (>80% filled-pigmented achenes in undisturbed heads).

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NOTEWORTHY COLLECTIONS

ARIZONA

CENTRANTHUS RUBER (L.) DC. (VALERIANACEAE).—Cochise Co., Bisbee, edge of parkinglot near junction of Main St. and Commerce St., 5400' (1620 m), 14 Oct 1996, *Laferrière* 2679. (ARIZ, ASU).

Previous knowledge. Eurasian species sometimes cultivated as an ornamental. Occasionally established in the wild in California (Munz & Keck, 1959).

Significance. First time reported outside cultivation in Arizona.

SALPICHROA ORIGANIFOLIA (LAM.) BAILLON (SOLANACEAE).—Cochise Co., Bisbee, unkempt lawn at 129 Tombstone Canyon Road, 5400' (1620 m), 14 Oct 1996, *Laferrière* 2678 (ARIZ, ASU, MO).

Previous knowledge. Argentine species sometimes cultivated as an ornamental. Occasionally known from the wild in California and Florida but rarely producing fruit in North America (D'Arcy, MO, pers. comm.). The related *S. rhomboidea* (Gill. & Hook.) Miers is a difficult weed in parts of California (Munz & Keck, 1991).

Significance. First time reported outside cultivation in Arizona.

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A NEW SUBSPECIES OF *CLARKIA MILDREDIAE*
(ONAGRACEAE)

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ABSTRACT

Clarkia mildrediae subsp. *lutescens* is a newly described subspecies that is readily distinguished from subsp. *mildrediae* by the color of its anthers which may be bright yellow, yellow-orange, light orange or red-orange on different plants while those of subsp. *mildrediae* are magenta. Subspecies *lutescens* has a separate and nonoverlapping geographical distribution primarily in Butte and Plumas Counties where subsp. *mildrediae* is also found. Within subsp. *lutescens*, the proportion of plants with bright yellow anthers varies among populations from 98% to none. Bright yellow is homozygous and true breeding and is allelic to red-orange. Plants from populations with high proportions of bright yellow anthers also have shorter and narrower petals. Hybrids between the two subspecies are fully fertile.

Heller (1940) first distinguished *Clarkia mildrediae* (Heller) Lewis and Lewis as *Phaeostoma mildredae* from *P. atropurpureum* Heller, later included in the widespread *C. rhomboidea* Douglas (Lewis and Lewis 1955), on the basis of its larger flowers and later flowering. Lewis and Lewis (1955) determined that *P. mildredae* ($n = 7$) was one of the diploid parents of *C. rhomboidea* (the other being *C. virgata* Greene [$n = 5$]) and transferred it to *Clarkia* (Lewis and Lewis 1953). The relationship was proven by the finding (reported in Mosquin 1964) that experimental triploid hybrids between *C. mildrediae* and *C. rhomboidea* showed seven bivalents and five univalents at meiosis and those between *C. virgata* and *C. rhomboidea* showed five bivalents and seven univalents. The three species were recognized as *Clarkia* sect. *Myxocarpa* (Lewis and Lewis 1955). At that time, *C. mildrediae* was known only from a few localities on the North Fork of the Feather River in Butte and Plumas Counties and from the vicinity of Shasta Lake (Shasta County) to the north. Small (1971a, b) segregated the northern populations, by then extended to Trinity County, as *C. borealis* because of their virgate habit and lavender petals which differentiated them from *C. mildrediae* and because of the substantial differences between them in chromosomal arrangement which rendered their hybrids sterile. We

have been studying the species of sect. *Myxocarpa* (Gottlieb and Janeway 1995; Gottlieb and Ford unpublished) and our field work has led to the discovery of a new subspecies of *C. mildrediae* that we describe here as subsp. *lutescens*. The new subspecies has a separate and non-overlapping distribution, relative to subsp. *mildrediae*, in Butte and Plumas counties, and differs conspicuously in anther color and several other floral traits. Both subspecies are out-crossing and have the same chromosome number.

Anther color and genetics. Anthers of subsp. *mildrediae* are magenta and pollen is blue or blue-gray. Anthers of subsp. *lutescens* may be bright yellow, yellow-orange, light orange, or red-orange. Anther color is constant on each plant but may differ among plants within and between populations of subsp. *lutescens* (see below). In general, pollen color is correlated with anther color. Bright yellow anthers always have bright yellow pollen. Orange anthers are associated with tan or gray pollen, often with a yellow tinge, that sometimes darkens as the flower ages. Pollen of inner (epipetalous) anthers may initially appear yellow, darkening to tan, while pollen of the outer anthers may initially appear tan, darkening to a tan-gray, but never becoming blue or blue-gray. Anthers of subsp. *lutescens* are the same length as those of subsp. *mildrediae*, the outer ones generally 8–10 mm. They project forward of the four reddish-purple petals as in subsp. *mildrediae*, but their contrasting color, particularly when bright yellow, is an elegant and notable feature.

A preliminary genetic analysis of anther color has been carried out. Self-pollinated progeny of a plant grown from field-collected seed from subsp. *lutescens* population 4412 that had yellow-orange anthers and tan-yellow pollen showed bright yellow, yellow-orange, or orange anthers. Progeny with bright yellow and yellow-orange anthers were self-pollinated. Yellow-orange segregated progeny of three types: 13 bright yellow, 23 yellow-orange, and 12 orange anthers, suggesting that anther color in this cross was controlled by two alleles at a single locus and that the test plant was heterozygous. The progeny from plants with bright yellow anthers and pollen bred true, suggesting they were homozygous.

Experimental hybrids between subsp. *mildrediae* and subsp. *lutescens* have anthers and pollen of various colors depending on the allelic state of the controlling loci. To date, only a few crosses of this type have been grown. Magenta shows complete or incomplete dominance with orange and yellow in different crosses. The appearance of plants with magenta anthers and bright yellow pollen (a phenotype not observed in nature) in some progenies from interspecific crosses suggests that the color differences between the subspecies are governed by at least two loci.

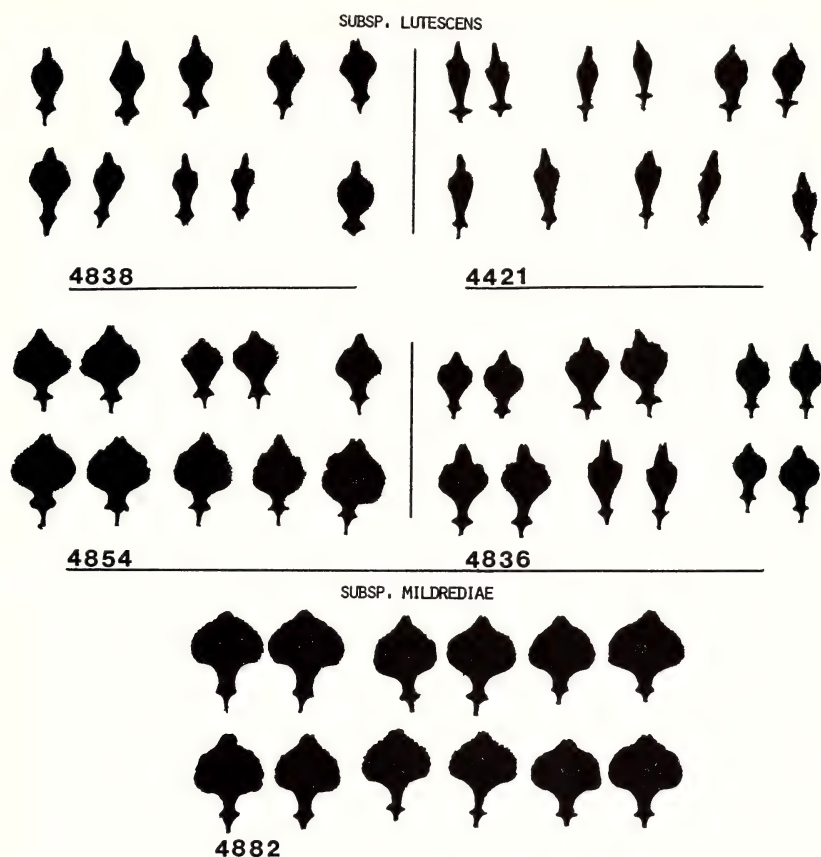


FIG. 1. Silhouettes of flower petals from representative populations of both subspecies of *C. mildrediae* grown in the greenhouse at Davis. For each plant, one petal was taken from both the first and second flower to open, on the day the stigma became receptive (usually three days after anthesis) because the petals are fully expanded then. The petals were placed on 3×5 cards under scotch tape which nicely preserves their size and shape. They were then xeroxed and the outlines filled in with black ink. Petals from five or six plants of each population are shown.

Petal shape. Petals of *C. mildrediae* have a deltoid or rounded limb that narrows into a claw with a pair of prominent lateral lobes above the slender base (Fig. 1). Petals from plants of numerous populations of both subspecies were measured in the field (Table 1) and also in the greenhouse (data not shown). Those of subsp. *mildrediae* are larger and broader. Within subsp. *lutescens*, plants from populations that have high proportions of light orange to red-orange anthers have nearly the same length and width as those of subsp. *mildrediae*. However, plants from populations that have predominantly bright yellow anthers and pollen, for example, populations

TABLE 1. PETAL LENGTH AND WIDTH COMPARISONS. Values reported (in mm) are means \pm 95% confidence limits for the population with the largest and the one with the smallest mean for each subspecies, with sample sizes in parentheses. Field measurements were of the second most recently opened flower which was generally one of the first three flowers on the inflorescence. The petals on each measured flower were fully expanded. Measurements were made in seven populations of *C. mildrediae* subsp. *mildrediae* and 13 of subsp. *lutescens*; sample sizes vary from 3 to 19 plants per population.

| subsp. <i>lutescens</i> | | | subsp. <i>mildrediae</i> | |
|-------------------------|-----------|----------------------|--------------------------|---------------------|
| Length | Pop. 4684 | 20.5 \pm 1.0 (10) | Pop. 4882 | 21.1 \pm 0.6 (14) |
| | Pop. 4837 | 16.1 \pm 0.6 (10) | Pop. 4681 | 18.8 \pm 0.7 (14) |
| | All pop. | 17.8 \pm 0.3 (130) | All pop. | 20.1 \pm 0.3 (88) |
| Width | Pop. 4693 | 14.9 \pm 1.4 (10) | Pop. 4882 | 16.7 \pm 0.8 (14) |
| | Pop. 4837 | 7.7 \pm 0.9 (10) | Pop. 4679 | 12.5 \pm 1.1 (8) |
| | All pop. | 11.6 \pm 0.4 (130) | All pop. | 14.9 \pm 0.5 (88) |

4421 and 4839 (Table 2), have shorter and significantly narrower petals (Fig. 1). The basis of this correlation has not yet been studied.

Geographical distribution. *Clarkia mildrediae* is distributed nearly entirely within Butte and Plumas Counties, with a few outlying locations in adjacent Yuba and Sierra Counties, east of Sly Creek Reservoir (Fig. 2). The subspecies are entirely allopatric and have not been found growing intermixed at any locality. Subspecies *lutescens* occurs in openings in the Yellow Pine forest and adjacent habitats from the North Fork of the Feather River, south and east of Pulga, and east to Big Creek (east of Bucks Lake) and south across the drainage of the Middle and South Forks of the Feather River to Canyon Creek, a tributary of the North Yuba River. Subspecies *mildrediae* occurs along the North Fork of the Feather River south of Belden, and north and west to the West Branch of the Feather River in the vicinity of Stirling City. Overall, its distribution is northwest of that of subsp. *lutescens*. In two areas, near Pulga on the North

TABLE 2. PROPORTION OF PLANTS WITH BRIGHT YELLOW ANTHERS AND POLLEN IN POPULATIONS OF *C. MILDREDIAE* SUBSP. *LUTESCENS*. Collections are those of LPJ.

| Population | Number plants sampled | % bright yellow |
|------------|-----------------------------|--------------------|
| 4839 | 100 | 98 |
| 4421 | 50 | 98 |
| 4838 | 50 | 89 |
| 4429 | 41 | 34 |
| 4836 | 50 | 28 |
| 4854 | 108 | 3 |
| 4881 | 50 | 0 |
| 4687 | 40 | 0 |

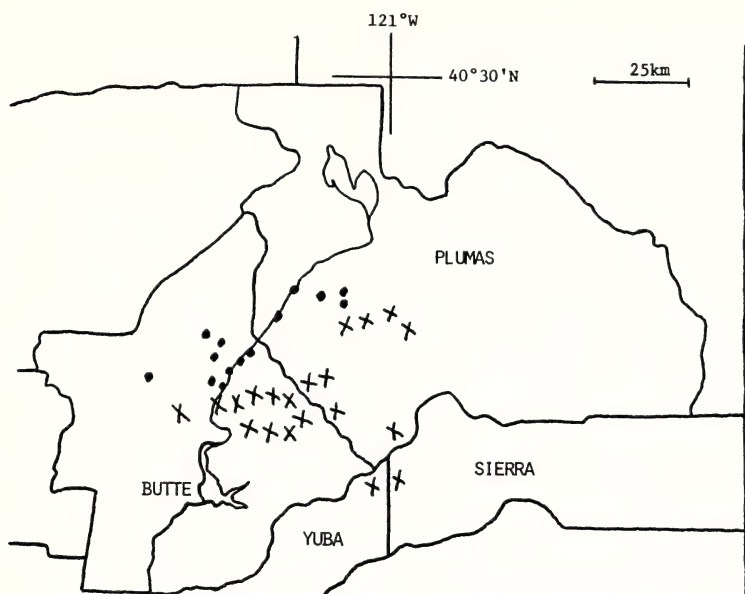


FIG. 2. Outline map of Butte, Plumas, and adjacent counties to show locations of collected populations of *C. mildrediae*. The North Fork of the Feather River is shown. Dots mark subsp. *mildrediae* and crosses mark subsp. *lutescens*.

Fork of the Feather River and southeast of Bucks Lake, populations of the two subspecies occur within several miles of each other.

In general, neither subspecies is known north or east of the vicinity of the Pacific Crest Trail in central Plumas County. Rainfall maps of the Plumas National Forest (Schultz and Benoit 1980) show that both subspecies are found in a region with mean annual precipitation greater than 145 cm; to the west and east of their distribution, the precipitation decreases rapidly. Both subspecies may be found in granitic, metamorphic or volcanic substrates and in elevations between 450 and 1700 meters.

As noted previously, populations of subsp. *lutescens* differ in the proportion of plants having different anther colors. Because bright yellow appears to be fully recessive to other colors and because this color can be readily identified, we scored the proportion of bright yellow in eight populations (Table 2). The proportion varied from 98% in populations 4421 and 4839 in the southwestern part of the distribution to zero or near zero in the northern and eastern portion. Populations that have predominantly bright yellow anthers seem to be restricted to Butte County.

Reproductive relationship. Pollen viability was examined in F_1 plants produced by crossing four pairs of populations representing

the two subspecies. The F_1 plants were vigorous and more than 98% of their pollen was stainable with acetocarmine and had a normal three-pored appearance. The plants set abundant seed after experimental pollination. Thus, the subspecies are fully interfertile and there is no evidence that they differ in chromosomal arrangement.

Conclusions. *Clarkia mildrediae* subsp. *lutescens* is readily distinguished from subsp. *mildrediae* by the color of its anthers and by the narrower petals in populations that have a high proportion of bright yellow anthers. Subspecies *lutescens* has a separate and non-overlapping geographical distribution in Butte and Plumas Counties where subsp. *mildrediae* is also found. The two have the same chromosome number and apparently the same chromosomal arrangement since their hybrids are fully fertile.

Subspecies *lutescens* was not recognized before now because previous students of *Clarkia* had not collected in its rugged territory. *Clarkia stellata* Mosquin, a predominantly self-fertilizing species that appears to have been derived from *C. mildrediae* (Mosquin 1962; Small 1971b) and is distributed in the same region of the northern Sierra Nevada, is probably derived from subsp. *lutescens* since both have yellow anthers and yellow pollen. We have designated the new taxon subsp. *lutescens* because the anthers, varying from bright yellow to red-orange on different plants, are its most distinctive feature.

TAXONOMY

***Clarkia mildrediae* (Heller) Lewis and Lewis subsp. *lutescens* Gottlieb and Janeway, subsp. nov.**—TYPE: USA, California, Butte County, Plumas National Forest Road 28 at Chino Creek, 7 July 1995, *Janeway 4837* (Holotype, JEPS, Isotypes, CHSC, DAV, RSA).

A *C. mildrediae* (Heller) Lewis & Lewis subsp. *mildrediae* dif-
fert: antheris varians individuís luteis, flavis aurantiacis, aremeni-
acis, o rubris aurantiacis; petalorum limbo 7–16 mm lato.

Differs from *C. mildrediae* (Heller) Lewis & Lewis subsp. *mildrediae*: anthers of different individuals yellow, yellow-orange, orange-red, or red; petal limbs 7–16 mm wide.

Paratypes. USA, California, Butte County, on road crossing (Plumas N.F. Road 28) of Last Chance Creek, 28 July 1982, *Schlising and Tarp 4358* (CHSC); along Bean Creek Road, ca. $\frac{3}{4}$ mi SW of Little Bald Rock, 29 June 1988, *Ahart 6102* (CAS, CHSC, MO); along French Creek Road 2.6 mi from Oroville-Quincy Hwy, 1 July 1993, *Janeway 4412* (CHSC, DAV); along French Creek Road 4.1 mi from Oroville-Quincy Hwy, 1 July 1993, *Janeway 4413* (CAS, CHSC); at the type locality Plumas N. F. Road 28 at Chino Creek,

2 July 1993, *Janeway 4421* (CAS, MO); 1.3 mi S-SW of Hungry Hunt Peak, 2 July 1993, *Janeway 4426* (CAS, CHSC); W end of Watson Ridge, 6 July 1993, *Janeway 4429* (CHSC, DAV); between Haphazard Creek and Baker and Foreman Creeks, 7 July 1994, *Janeway 4684* (CHSC); 1.3 mi S-SW of Hungry Hunt Peak, 7 July 1995, *Janeway 4836* (GH, MO, RSA, US); along French Creek Road 4.1 mi from Oroville-Quincy Hwy, 7 July 1995, *Janeway 4838* (LA, MO); between Mountain House, French Creek and Mosquito Creek, 7 July 1995, *Janeway 4839* (HSC, NY, RENO, US); Plumas County. Oroville-Quincy Hwy, 0.9 mi W of Grizzly Creek, 22 July 1993, *Janeway 4469* (CHSC, DAV); Hartman Bar Ridge, 8 July 1994, *Janeway 4687* (CHSC, DAV, JEPS, MO); between Lookout Rock and Middle Fork Feather River, 13 July 1994, *Janeway 4693* (CHSC, JEPS); Oroville-Quincy Hwy, 0.9 mi W of Grizzly Creek, 29 July 1995, *Janeway 4881* (CAS, MO, RSA, US); Sierra County. Rock Creek 0.3 mi NW of Canyon Creek, 1 July 1994, *Janeway 4676* (CHSC); Yuba County. Slate Creek, 3 mi NE of Strawberry Valley, 1 July 1994, *Janeway 4674* (CAS, CHSC); Slate Creek, 3 mi NE of Strawberry Valley, 15 July 1995, *Janeway 4854* (GH, MO, RSA, US).

Collection numbers and localities of the populations of subsp. *mildrediae* cited in the text are identified below (all collections are those of Janeway): *4679*: 0.7 mi E-SE of Flea Mountain (CHSC); *4681*: Granite Ridge, along the Concow Road (CHSC); *4720*: ¼ mi W of Bear Ranch Creek Falls in North Fork Feather River Canyon; *4858*: 0.8 mi NW of Oak Point (E of Stirling City) (CHSC, GH, NY, US); *4882*: Pipeline Road, NW of Bucks Lake (CHSC, DAV, JEPS, RSA).

ACKNOWLEDGMENTS

We thank Kent Holsinger for assistance with the Latin diagnosis, and the curators of the following herbaria for loans of specimens and access to their collections: CAS, CHSC, DS, GH, JEPS, HSC, LA, MO, NY, OSC, POM, RENO, RSA, UC, US. This study was supported in part by the Plumas National Forest (LPJ) and by National Science Foundation grant BSR 91-06831 (LDG).

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PHENETIC ANALYSIS OF *ARCTOSTAPHYLOS PARRYANA* I. TWO NEW BURL-FORMING SUBSPECIES

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ABSTRACT

Arctostaphylos parryana Lemmon is here circumscribed as a species that includes both non-burl forming and burl-forming taxa. Principal components analysis based on 50 phenetic characters was used to support the recognition of two new subspecies. *Arctostaphylos parryana* subsp. **tumescens** Keeley, Boykin, & Massihi is morphologically similar to the nominate subspecies but is distinct in its geographical and ecological distribution, presence of a globose basal burl and erect growth form. *Arctostaphylos parryana* subsp. **deserticum** Keeley, Boykin, & Massihi also differs from the nominate subspecies in the presence of a basal burl, and differs from both other subspecies in its intensely glaucous, slightly narrower leaves and smaller fruits and desert chaparral habitat. These subspecies increase the range of *A. parryana* by >150 km southeastward, and to the San Bernardino, San Jacinto, Santa Rosa, and San Ysidro mountain ranges and to Riverside and San Diego counties.

As presented in previous taxonomic treatments, *Arctostaphylos parryana* Lemmon is a polyploid, non-burl forming manzanita with a mounded growth form (Fig. 1) and typically is distributed as scattered shrubs in arid woodlands and montane forests (Adams 1940, Wells 1993). It ranges from Lockwood Valley and Mt. Pinos in eastern Ventura County to the southern Tehachipi Mountains of Kern County and northern and eastern portions of the San Gabriel Mountains in Los Angeles and San Bernardino counties. It is morphologically distinguished by its tomentose branchlets and rachises, reduced floral bracts, and round fruits with a solid endocarp stone. Recently we have made extensive collections of manzanitas with these characteristics, indicating clear affinities to *A. parryana*, and in this paper we will show

- (1) A significant increase in the range of this species east and south,



FIG. 1. Mounded growth form of typical *A. parryana*.

- (2) that the species includes many burl-forming populations,
- (3) these populations are best treated as subspecies, and in a subsequent contribution (Keeley et al. in preparation) we will show
- (4) The pattern of variation in *A. parryana* suggests the hypothesis that there has been widespread hybridization and introgression from *A. glandulosa* Eastwood, and
- (5) evidence that *A. gabrielensis* Wells comprises a single population along a cline from *A. parryana* to *A. glandulosa*.

STUDY SITES

Distribution of taxa considered here is shown in Figure 2 and names, locality data, and sample sizes are in Table 1. Here the term "population" is used broadly to refer to both distinct populations as well as metapopulations (groups of populations separated by areas of unsuitable habitat).

METHODS

Extensive collections of all populations were made in late summer and autumn in order to obtain both current-year fruits and nascent inflorescences for the following year. These are critical characters in manzanita taxonomy and only specimens with both present were included in our phenetic analysis. The combined presence of these two characters was a determining factor in the final sample size for

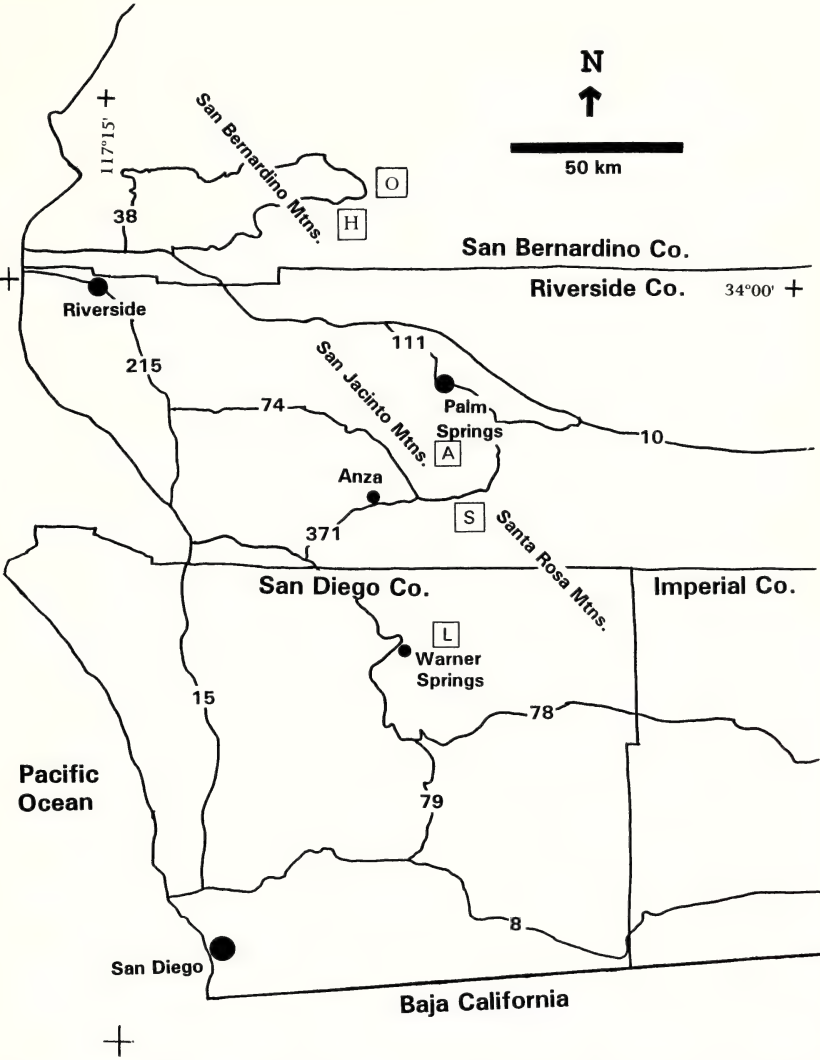


FIG. 2. Eastern distribution of populations studied here. See Table 1 for location data and sample sizes.

each population. A total of 50 characters were recorded for each plant sample, which were subsequently retained as vouchers and deposited at RSA. Fifteen quantitative, 2 meristic, and 30 qualitative characters, and 3 calculated ratios were recorded from each specimen. Qualitative characters were ranked from 1 to 5. Quantitative characters were represented by the mean of two samples from each

TABLE 1. POPULATIONS OF *ARCTOSTAPHYLOS* INCLUDED IN THIS STUDY.

| | Code | Sample size | Burl | County or Country | Mtn. Range | Location | Elevation (m) |
|------------------------|------|-------------|------|------------------------------|------------------------------|---|--|
| <i>A. parryana</i> | | | | | | | |
| "Ventura" | v | 39 | No | Ventura/Kern | Tehachapi & Mt. Pinos region | Lockwood Valley Mutau Flat Mt. Pinos | 1500-1700 1500-1700 1900 |
| "San Gabriels" | g | 68 | No | Los Angeles & San Bernardino | San Gabriel | Cerro Noroeste Sulphur Spgs. Wrightwood Pacifico Crystal Lake | 1900-2400 1600-1700 2000 2000 1850 |
| "Onyx" | o | 59 | No | San Bernardino | San Bernardino | San Antonio Cyn NE Onyx Peak | 1900 2400 |
| "Heartbar" | H | 58 | Yes | San Bernardino | San Bernardino | Rattlesnake Cyn | 2100 |
| "Andreas" | A | 20 | Yes | Riverside | San Jacinto | SW Heartbar Pk | 2100-2300 |
| "Santa Rosa" | S | 66 | Yes | Riverside | Santa Rosa | Andreas Cyn | 2000-2100 |
| "Los Coyotes" | L | 30 | Yes | San Diego | San Ysidro | N/W Sta. Rosa Mtn. Borrego-Palm Cyn Indian Cyn | 1600-2200 1300-1700 |
| <i>A. peninsularis</i> | R | 20 | Yes | Baja California | San Pedro Martir | W of National Park | 1000-2000 |
| <i>A. glandulosa</i> | C | 30 | Yes | San Diego | San Marcos | Encinitas-Econdido | 100-500 |

specimen. All character states were standardized by transforming each variable with a z-score obtained by subtracting each observation from the mean of all individuals, and dividing by the standard deviation. This data matrix was used for ordination with principal components analysis using SYSTAT for Windows, Version 5.05 (Evanston, IL).

Stomatal density on ad- and abaxial surfaces were determined on a sub-sample from each population from epidermal peels made of clear nail polish and examined under 40 \times . Since there was relatively little inter-population variability these data were not taken from every specimen and were not used in the principal components analysis. Chromosome counts were made on some populations from flower buds collected in late winter to early spring and preserved in 3:1 ethanol:glacial acetic acid. Anthers, not yet pigmented, were dissected out and squashed with aceto-carmin and examined at 100 \times . This character was likewise not used in the principal components analysis. Additionally, characters with zero variance were automatically excluded from the principal components analysis.

RESULTS

San Bernardino Mountains. Although previously unrecorded from this range, there is an extensive population of *A. parryana* between 2100 and 2300 m on the western and southern slopes of Heartbar Peak (Table 1 and Fig. 2). These plants are approximately 80 km E of the known range of *A. parryana* in San Antonio Canyon in the San Gabriel Mountains. They are clearly related to *A. parryana* in their bright green foliage, tomentose branchlets and rachises, and relatively large round glabrous fruits with a solid stone (Fig. 3). However, the Heartbar Peak population differed significantly in that each shrub had a well-developed basal burl and lacked the mounded growth form of typical *A. parryana*. Further, the population covered several hectares of densely packed erect manzanitas in association with other chaparral shrubs. This contrasts sharply with the mounded growth form and scattered distribution in woodland and forest gaps, typical of non-burl forming *A. parryana*. The Heartbar population is largely restricted to chaparral on steep slopes and is replaced by *A. patula* in forest gaps in the valley bottom.

Principal components analysis comparing the phenetic traits (excluding the burl and growth form characters) of this Heartbar Peak population (H) with typical *A. parryana* from Ventura County (v) and the San Gabriel Mountains (g) (see Table 1 for location data) verifies the morphological similarity between the newly discovered Heartbar population and typical *A. parryana* (Fig. 4). Although these populations overlapped a great deal, there was some separation along the factor 1 axis, which accounted for 11% of the total vari-



FIG. 3. Large round glabrous fruits of the Heartbar *A. parryana*.

ance. Based on the component loadings, which indicate the extent each character contributes to the variance, the primary difference between these populations was the slightly sparser pubescence and somewhat larger fruits in the Heartbar population. Despite the phenetic similarity, the Heartbar manzanitas were clearly distinguishable from typical *A. parryana* by the prominent basal burl, erect growth habit, and affinity for chaparral.

On the eastern face of the San Bernardino Mountains, between 2100 and 2400 m, a widely scattered population of non-burl forming *A. parryana* was also collected, E of Onyx Peak and extending several km N to Rattlesnake Canyon (Table 1 and Fig. 2). As with

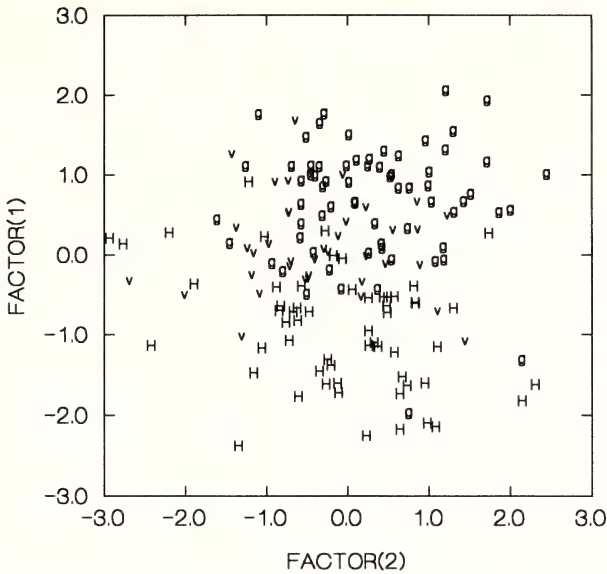


FIG. 4. Plot of the first two factors in the principal component analysis comparing the burl-forming Heartbar manzanitas (H), and typical non-burl-forming *A. parryana* from Ventura County (v) and the San Gabriel Mountains (g). See Table 1 for locations and sample sizes and Table 2 for factor 1 loadings, which explained 11% of the total variance.

typical *A. parryana*, these plants had a mounded growth form and generally were associated with pinyon-juniper woodland. Principal components analysis showed that these manzanitas (o) were largely indistinguishable from typical *A. parryana* from Ventura County (v) and the San Gabriel Mountains (g) (Fig. 5). Separation along the factor 1 axis accounted for 12% of the total variance, primarily contributed by slightly larger fruits in the Onyx populations. Otherwise, this population greatly resembled typical *A. parryana*, however, it represents approximately a 100 km eastward range extension for *A. parryana*.

San Jacinto, Santa Rosa, and San Ysidro ranges. Burl-forming manzanitas with tomentose branchlets, reduced floral bracts, and round solid fruits, indicating affinities to *A. parryana*, are also found in three mountain ranges south of the San Bernardino Mountains (Table 1 and Fig. 2). All of these populations occur in chaparral near the desert edge and many are accessible only by trail.

The most extensive populations we have found to-date are at the northern end of the Santa Rosa Mountain Range (Riverside County), between 1600 and 2200 m, on the western and northern sides of Santa Rosa Mountain. Principal components analysis (not shown)

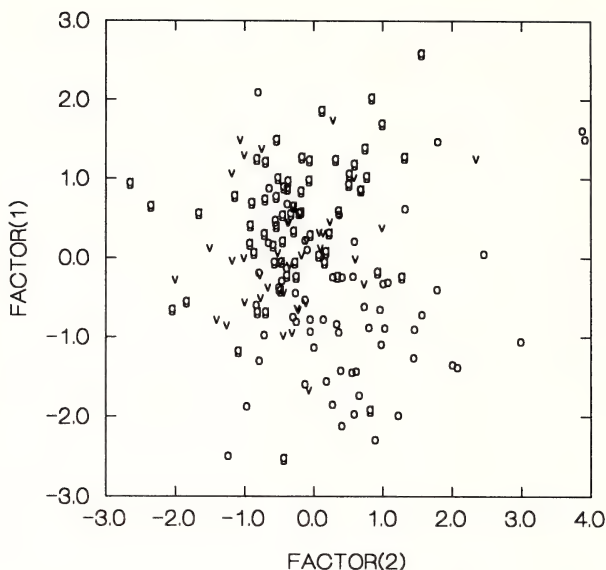


FIG. 5. Plot of the first two factors in the principal component analysis comparing the non-burl-forming *A. parryana* populations from Ventura County (v), San Gabriel Mountains (g), and E of Onyx Peak in the San Bernardino Mountains (o). See Table 1 for locations and sample sizes and Table 2 for factor loadings; factor 1 explained 12% of the total variance.

of four widely separated populations on Santa Rosa Mountain indicated extensive morphological overlap between these populations, thus all populations were treated together as a metapopulation.

Principal components analysis showed that the burl-forming Santa Rosa Mountain (S) manzanitas are well separated from the non-burl forming Ventura (v) plants and overlap slightly with the burl-forming Heartbar (H) plants (Fig. 6). The Santa Rosa Mountain manzanitas share with the Heartbar plants the erect habit and basal burl but differ in having markedly smaller fruits and a preponderance of plants with very glaucous-white leaves, as indicated by the component loadings (Table 2). Overlap between the Santa Rosa Mountain and Heartbar populations (Fig. 6) is due to weakly glaucous shrubs at the higher elevations on Santa Rosa Mountain.

Other extensive burl-forming populations with affinities to *A. parryana* occur further south in the San Ysidro Mountains on the eastern border of the Los Coyotes Indian Reservation in San Diego County (L). These plants appear similar to the Santa Rosa Mountain plants but are strikingly unlike the Heartbar plants in their intensely glaucous and narrower leaves and smaller fruits. Principal components analysis indicates that the Los Coyotes populations are clearly separable from the

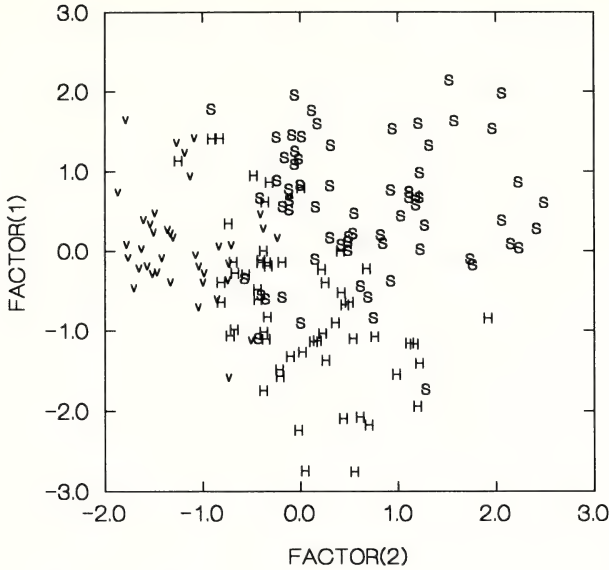


FIG. 6. Plot of the first two factors in the principal component analysis comparing the burl-forming Santa Rosa Mountain population (S) with the burl-forming Heartbar (H), and non-burl-forming Ventura County (v) and the San Gabriel Mountains (g) *A. parryana*. See Table 1 for locations and sample sizes and Table 2 for factor 1 loadings, which explained 10% of the total variance.

typical non-burl-forming *A. parryana* from Ventura County and distinct from the burl-forming *A. parryana* from Heartbar in the San Bernardino Mountains (Fig. 7). The factor 1 axis accounts for 17% of the total variance and component loadings indicate that shorter bract length and greater leaf glaucousness and scabrousness are most significant in separating these populations (Table 2).

Burl-forming *A. parryana* also occur on the desert slopes of the San Jacinto Mountains. One population from Andreas Canyon (A) more resembled Santa Rosa and Los Coyotes plants than San Bernardino plants. Principal components analysis (not shown) indicated that these manzanitas were clearly separable from the Heartbar population and Ventura County population, and the factor 1 axis accounted for 21% of the total variance.

Comparison with other Arctostaphylos species. Several characteristics of these burl-forming *A. parryana* populations, e.g., round glabrous fruits with solid stones and glaucous leaves, burls, and desert affinity in some, are shared with the northern Baja California *A. peninsularis* Wells. These *A. parryana* populations also share the burl-forming habit with the widespread coastal range species *A. glandulosa*. Principal components analysis comparing the burl-form-

TABLE 2. CHARACTERS USED IN PRINCIPLE COMPONENTS ANALYSIS AND COMPONENT LOADINGS FOR FACTOR 1 FOR FIGURES 4, 5, 6, 7, & 8. N.I. = not included.

| Character | Fig. 4 | Fig. 5 | Fig. 6 | Fig. 7 | Fig. 8 |
|--------------------------|--------|--------|--------|--------|--------|
| Burl | N.I. | N.I. | 0.193 | 0.284 | N.I. |
| Leaf blade length | -0.132 | -0.090 | -0.154 | 0.243 | 0.356 |
| Leaf blade width | 0.066 | 0.425 | -0.415 | -0.188 | -0.005 |
| Ratio leaf width/length | -0.219 | -0.512 | 0.370 | 0.462 | 0.430 |
| Basal angle | -0.141 | -0.474 | 0.128 | 0.260 | 0.218 |
| Apical angle | -0.156 | -0.431 | 0.221 | 0.347 | 0.240 |
| Blade shape | 0.053 | -0.327 | 0.076 | -0.214 | 0.036 |
| Petiole length | -0.250 | 0.061 | -0.026 | 0.192 | 0.026 |
| Leaf color | -0.570 | -0.394 | 0.178 | 0.315 | 0.410 |
| Leaf glaucousness | 0.003 | -0.158 | -0.571 | -0.816 | -0.088 |
| Leaf scabrousness | -0.302 | -0.143 | 0.399 | 0.770 | 0.593 |
| Branchlet pubescence | -0.651 | -0.550 | 0.378 | 0.764 | 0.890 |
| Petiole pubescence | -0.624 | -0.572 | 0.190 | 0.682 | 0.881 |
| Leaf blade pubescence | | | | | |
| Mature leaf | -0.307 | -0.207 | 0.432 | 0.300 | 0.765 |
| Immature leaf | -0.311 | -0.309 | 0.205 | 0.579 | 0.812 |
| Rachis pubescence | -0.576 | -0.467 | 0.380 | 0.728 | 0.850 |
| Pedicle pubescence | -0.037 | -0.081 | 0.321 | 0.612 | 0.817 |
| Branchlet glandularity | 0.503 | 0.232 | 0.151 | 0.476 | 0.885 |
| Petiole glandularity | 0.147 | -0.023 | 0.187 | 0.587 | 0.910 |
| Leaf blade glandularity | N.I. | N.I. | 0.185 | 0.182 | 0.843 |
| Rachis glandularity | 0.464 | 0.163 | 0.183 | 0.258 | 0.876 |
| Pedicle glandularity | 0.176 | N.I. | 0.377 | 0.466 | 0.887 |
| Inflorescence length | 0.063 | 0.201 | 0.154 | 0.020 | 0.237 |
| # of rachis branches | 0.513 | 0.269 | -0.132 | -0.142 | -0.023 |
| Bract spacing | 0.503 | 0.176 | -0.245 | -0.156 | -0.042 |
| Bract keel | 0.127 | 0.289 | 0.057 | 0.185 | -0.602 |
| Bract shape | 0.166 | 0.132 | -0.057 | -0.236 | -0.781 |
| Bract marcescence | -0.417 | -0.301 | -0.287 | 0.239 | -0.276 |
| Bract reflexed | -0.079 | -0.093 | -0.037 | 0.407 | 0.574 |
| Bract length, subtending | | | | | |
| Inflorescence | -0.128 | 0.170 | 0.609 | 0.851 | 0.622 |
| Flower bud | -0.329 | -0.139 | 0.161 | 0.104 | 0.674 |
| Pedicle length | -0.269 | 0.160 | 0.011 | 0.480 | -0.037 |
| Sepal shape | -0.364 | -0.296 | 0.420 | -0.015 | -0.617 |
| Sepal reflexed | 0.071 | 0.022 | 0.342 | 0.487 | -0.119 |
| Fruit color | 0.084 | -0.033 | -0.003 | 0.517 | -0.170 |
| Fruit height | 0.307 | 0.525 | -0.519 | -0.406 | -0.727 |
| Fruit width | 0.477 | 0.599 | -0.607 | -0.305 | -0.438 |
| Fruit width/fruit height | 0.147 | 0.061 | -0.103 | 0.200 | 0.585 |
| Fruit weight | 0.477 | 0.700 | -0.706 | -0.482 | -0.597 |
| Fruit pubescence | 0.181 | 0.094 | 0.044 | 0.588 | 0.486 |
| Fruit glandularity | N.I. | N.I. | 0.171 | 0.267 | 0.723 |
| Pericarp weight | 0.453 | 0.530 | -0.399 | -0.277 | -0.507 |
| Endocarp weight | 0.469 | 0.599 | -0.707 | -0.493 | -0.541 |
| Endocarp height | 0.400 | 0.466 | -0.472 | -0.159 | -0.677 |
| Endocarp width | 0.510 | 0.566 | -0.661 | -0.322 | -0.563 |
| Endocarp apiculate | -0.229 | -0.199 | -0.011 | -0.089 | -0.590 |
| Mesocarp texture | 0.170 | 0.174 | -0.115 | -0.157 | -0.370 |
| Endocarp segments | -0.305 | -0.286 | 0.128 | 0.296 | 0.710 |
| Endocarp lateral ridges | -0.433 | -0.463 | 0.027 | 0.063 | -0.190 |
| Endocarp sculpturing | -0.287 | -0.332 | 0.035 | 0.016 | -0.439 |

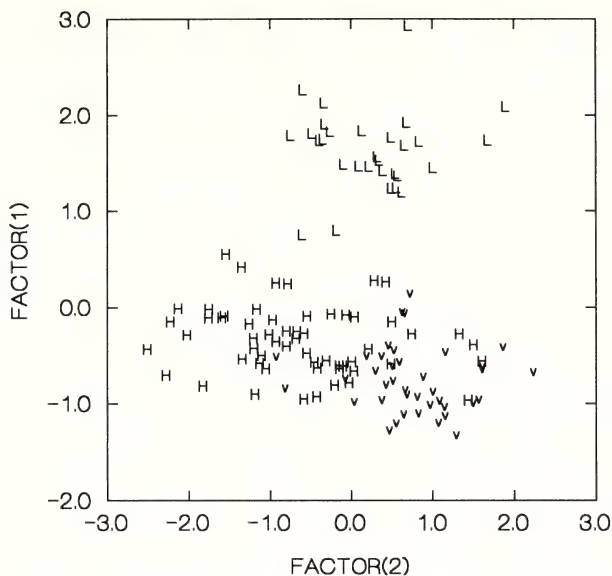


FIG. 7. Plot of the first two factors in the principal component analysis comparing the burl-forming Los Coyotes population (L) with the burl-forming Heartbar (H), and non-burl-forming Ventura County (v) *A. parryana*. See Table 1 for locations and sample sizes and Table 2 for factor 1 loadings, which explained 17% of the total variance.

ing *A. parryana* taxa (H,A,S,L) with burl-forming *A. peninsularis* (R) from the San Pedro Mártir and *A. glandulosa* (C) from the coastal ranges of San Diego County is shown in Figure 8. The strongest separation was on the factor 1 axis, which accounted for 33% of the variance and illustrates that these *A. parryana* taxa are clearly distinct from *A. glandulosa* and *A. peninsularis*, based largely on indument and fruit characters (Table 2).

Chromosome number. Two chromosome counts on the burl-forming Heartbar *A. parryana* gave counts of $n = 26$, indicating they were tetraploid. Two counts for non-burl-forming Onyx Peak and Rattlesnake Canyon specimens likewise gave counts of $n = 26$, and one count for a Santa Rosa Mountain plant gave a count of $n = 26$. Three counts for Los Coyotes plants gave both $n = 13$ and $n = 26$.

DISCUSSION

These studies greatly change our perception of *A. parryana*, in terms of its geographical range, ecology, and range of phenetic variation. The Heartbar population is morphologically quite close to the type, although fruits are somewhat larger (Fig. 3). This population

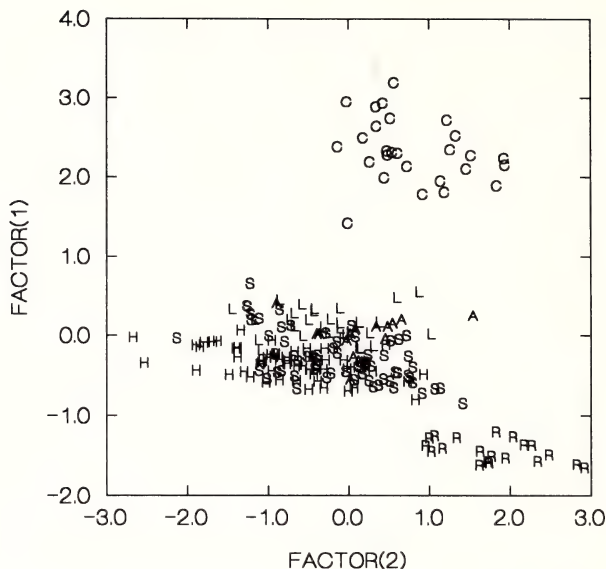


FIG. 8. Plot of the first two factors in the principal component analysis comparing the burl-forming populations of *A. parryana* (H = Heartbar, S = Santa Rosa, L = Los Coyotes, A = Andreas Cyn) with the burl-forming *A. glandulosa* (C) and burl-forming *A. peninsularis* (R). See Table 1 for locations and sample sizes and Table 2 for factor 1 loadings, which explained 33% of the total variance.

is markedly unlike typical *A. parryana* in having a well-developed basal burl, an erect growth form and distribution in dense montane chaparral. This contrasts markedly with *A. parryana* throughout its range where it is a non-burl-forming shrub with a mounded growth form (Fig. 1) and is distributed as scattered shrubs, in pinyon-juniper woodland or mixed conifer forests. We believe these differences are significant and the San Bernardino Mountains burl-forming plants should be recognized at the level of subspecies.

Burl-forming *A. parryana* in the ranges south of the San Bernardino Mountains are, however, phenetically quite distinct from the Heartbar population, most prominently in their intensely glaucous foliage, and they also have slightly narrower and more pointed leaves, and smaller fruits. Additionally, this taxon is ecologically distinct in its restriction to chaparral on the desert edge of the San Jacinto, Santa Rosa, and San Ysidro mountains. Therefore, we propose these glaucous-leaved manzanitas be treated as an additional subspecies.

TAXONOMIC TREATMENT

Arctostaphylos parryana* subsp. *tumescens J. Keeley, Boykin, & Massihi, subsp. nov.—TYPE: USA, California, San Bernardino

County, chaparral covered slopes on NW face of Heartbar Peak, S of Hwy 38, 2160 m, San Bernardino Mountains, 34°10', 116°45', 23 Sept 1992, *J. Keeley & M. Keeley 21436* (holotype, RSA; isotypes, CAS, SD, MO).

Frutices erecti, caudex tumescens, repullulans post combustum; drupae 10 mm diametro.

Erect shrub with large globose burl formed early in development and platform-like on older resprouted shrubs, in chaparral habitat. Fruits 10 mm diameter. $n = 26$ (A. Massihi and J. Keeley). The epithet recognizes the swollen basal burl.

Montane chaparral in eastern San Bernardino Mountains, from Heartbar Peak east, and in the San Gabriel Mountains, such as chaparral near Newcomb Ranch (*J. Keeley 20599*, RSA).

Paratypes. USA, California, San Bernardino County, Rd to Coon Crk., 5.0 km SE of Hwy 38, southern base of Heartbar Peak, 2310 m, 27 Sept 1992, *J. Keeley 21864* (RSA); ecotone of chaparral and *Quercus chrysolepis* woodland, SE face of Heartbar Peak, 2250 m, 25 October 1992, *J. E. Keeley 22305* (RSA).

Arctostaphylos parryana* subsp. *deserticum J. Keeley, Boykin, & Massihi, subsp. nov.—TYPE: USA, California, San Diego County, Middle Fork Borrego Palm Cyn., 3–4 km SE San Ignacio, E of Hot Springs Mountain, 1500 m, San Ysidro Mountains, 33°17', 116°30', 26 Sept 1992, *J. Keeley 21656* (holotype, RSA; isotypes, CAS, SD, MO).

Frutices erecti, caudex tumescens, repullulans post combustum; laminae glaucae, ellipticae, apices acuti; drupae 7–8 mm diametro.

Erect shrub with large globose burl formed early in development and platform-like on older resprouted shrubs, in chaparral near desert edge. Leaf blades narrow-elliptic with acute apices and moderately to intensely glaucous, fruits 7–8 mm diameter. $n = 13, 26$ (A. Massihi and J. Keeley). The epithet recognizes the consistent tendency of this taxon to be restricted to the desert edge of chaparral.

Chaparral at desert edge in San Diego and Riverside counties.

Paratypes. USA, California, San Diego County, Los Coyotes Indian Reservation, Indian Canyon, E. of Warner Springs, 1320 m, 10 April 1994, *Massihi, J. Keeley 25300* (RSA); S facing slopes E of Hot Springs Mountain, upper end of Choke Cherry Valley, Los Coyotes Indian Reservation, 1670 m, 18 September 1992, *J. Keeley 21326* (RSA); Riverside County, Road to Santa Rosa Mountain (7SO2), 2.5 km S of Hwy 74, 1640 m, Santa Rosa Mountains, 32°00', 116°30', 16 July 1992, *J. Keeley 16636* (RSA).

TABLE 3. *ARCTOSTAPHYLOS PARRYANA* SUBSPECIES COMPARISON. Mean \pm standard error. Glaucous scale: 1 = intensely glaucous - 5 = non-glaucous and lustrous. Scabrous scale: 1 = smooth - 5 = rough.

| Character | <i>A. parryana</i> ssp. <i>parryana</i> | <i>A. parryana</i> ssp. <i>tumescens</i> | <i>A. parryana</i> ssp. <i>deserticum</i> | <i>A. glandulosa</i> (coastal San Diego) | <i>A. peninsularis</i> (San Pedro Martir) |
|---|--|---|--|---|--|
| Sample size | 107 | 58 | 30 | 33 | 20 |
| Chromosome # | $n = 26$ | $n = 26$ | $n = 13, 26$ | $n = 26$ | ? |
| Burl | No | Yes | Yes | Yes | Yes |
| Leaves | | | | | |
| Length | 32 ± 1 | 32 ± 1 | 33 ± 1 | 37 ± 1 | 32 ± 1 |
| Length/width | 1.6 ± 0.0 | 1.5 ± 0.0 | 1.7 ± 0.0 | 1.8 ± 0.1 | 1.7 ± 0.0 |
| Apical angle | 39 ± 1 | 34 ± 1 | 44 ± 1 | 46 ± 2 | 44 ± 1 |
| Glaucous | 4.1 ± 0.1 | 4.0 ± 0.1 | 2.1 ± 0.1 | 2.8 ± 0.1 | 1.3 ± 0.1 |
| Scabrous | 1.2 ± 0.1 | 1.0 ± 0.1 | 2.2 ± 0.1 | 2.6 ± 0.2 | 1.0 ± 0.0 |
| Stomata | | | | | |
| Abaxial density (#/mm ²) | 24 ± 0 | 25 ± 0 | 21 ± 0 | 27 ± 1 | 25 ± 1 |
| Ratio | | | | | |
| abaxial/adaxial | 1.0 ± 0.0 | 1.1 ± 0.0 | 1.0 ± 0.0 | 1.4 ± 0.1 | 1.2 ± 0.1 |
| Branchlet indument | Tomentose | Tomentose | Tomentose | Hirsute Eglandular to intensely glandular | Glabrous |
| Lower Bract | | | | | |
| Length | 0.4 ± 0.1 | 0.1 ± 0.1 | 4.6 ± 0.2 | 6.3 ± 0.4 | 0.2 ± 0.2 |
| Fruits | | | | | |
| Width/height | 1.0 ± 0.0 | 1.0 ± 0.0 | 1.1 ± 0.0 | 1.5 ± 0.1 | 1.0 ± 0.0 |
| Mass (g) | 383 ± 9 | 447 ± 19 | 329 ± 17 | 145 ± 10 | 242 ± 19 |
| Pyrenes | 1.2 ± 0.0 | 1.1 ± 0.0 | 1.3 ± 0.1 | 3.1 ± 0.2 | 1.0 ± 0.0 |

CONCLUSIONS

Table 3 contrasts these newly described subspecies with *Arctostaphylos parryana* ssp. *parryana* and with other morphologically similar burl-forming species. Morphologically, *A. parryana* ssp. *tumescens* is nearly indistinguishable from the nominate subspecies and has diverged largely in habitat, growth form and the presence of a basal burl. Greater divergence is seen in *A. parryana* ssp. *deserticum* with several foliage characteristics tending towards those of *A. glandulosa*, with which it co-occurs on the western edge of its range. However, *A. parryana* ssp. *deserticum* has fruits that are more than double those of *A. glandulosa* and the round, mostly solid endocarp stones clearly distinguish it from that species.

ACKNOWLEDGMENTS

We thank Nancy James for her early unpublished report of a burl-forming manzanita from Heartbar Peak and Steve Boyd (RSA) for curating these collections.

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**METASTELMA MEXICANUM (ASCLEPIADACEAE): A NEW
COMBINATION AND RE-EVALUATION OF THE
STATUS OF *BASISTELMA* BARTLETT**

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ABSTRACT

Intensive collecting in southeastern Sonora, México has clarified the conspecific nature of *Cynanchum wigginsii* Shinnery [*Basistelma angustifolium* (Torr.) Bartlett] and *Basistelma mexicanum* (Brandegee) Bartlett. This species is known from apparently disjunct localities in central Sinaloa, southeastern Sonora, and the United States-México border region in Arizona and Sonora. Apparent distributional gaps between these population systems are probably due to insufficient botanical collecting rather than truly disjunct occurrences. The two entities that we treat as a single species were differentiated in the most recent treatment of these taxa by degree of recurvature of the apical anther appendages and the length of the style apex. These differences were based presumably on examination of very few specimens. Our examination of additional collections from a broad geographic area reveals that both characters vary on a local scale and do not covary consistently; thus recognition of two species is unwarranted. Acceptance of *Metastelma* R. Br. as a genus distinct from *Cynanchum* L. necessitates the new combination, ***Metastelma mexicanum*** (Brandegee) Fishbein & R. Levin. Although separated from *Metastelma* in previous treatments on the basis of the unusual elongate style apex, *M. mexicanum* is clearly a member of this genus; it possesses the comparatively delicate habit, small cuneate-based leaves, and minute flowers with simple corona scales characteristic of *Metastelma*.

RESUMEN

Colecciones intensivas del suroeste de Sonora, México han aclarado la esencia conspécifica de *Cynanchum wigginsii* Shinnery [*Basistelma angustifolium* (Torr.) Bartlett] y *Basistelma mexicanum* (Brandegee) Bartlett. Esta especie se ha encontrado en localidades aparentemente separadas en Sinaloa central, el suroeste de Sonora, y el área de la frontera entre los Estados Unidos y México en Arizona y Sonora. Estos aparentes vacíos distribucionales entre estas poblaciones están probablemente causados por colecciones insuficientes. Las dos especies que presentamos aquí como una especie única se diferenciaban de acuerdo en el estudio más reciente de estas especies por la cantidad de encorvadura de las añadiduras apicales de las anteras y la longitud del ápice del estilo. Estas diferencias estaban basadas probablemente en el estudio de pocos especímenes. Nuestro estudio de colecciones adicionales de una región más amplia revela que ambos caracteres varían a pequeña escala y no covarían constantemente; por esto el reconocimiento de dos especies no está justificado. La aceptación de *Metastelma* R. Br. como un género distinto de *Cynanchum* necesita la combinación nueva, ***Metastelma mexicanum*** (Brandegee) Fishbein & R. Levin. Aunque estaba separado de *Metastelma* en estudios anteriores por el insólito estilo ápice alargado,

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M. mexicanum es claramente un miembro de este género; tiene el hábito relativamente delicado, pequeñas hojas cuneadas, y flores diminutas con hojuelas sencillas de la corona que son características de *Metastelma*.

Metastelma R. Br. is a medium-sized genus of probably fewer than 100 species found in both hemispheres of the Americas (Stevens 1985; Liede and Meve 1997). Following Woodson (1941), *Metastelma* has been treated as part of a very broadly circumscribed *Cynanchum* L. by some North American workers (e.g., Standley and Williams 1969; Correll and Johnston 1970; Sundell 1981, 1994; Rossatti 1989). This highly inclusive treatment of *Cynanchum* has not met with general acceptance in North America, and *Metastelma* has been maintained by several systematists (e.g., Shreve and Wiggins 1964; Wiggins 1980; Stevens 1985, 1988). As noted by Liede and Meve (1997), South American workers have also inconsistently recognized *Metastelma*. Recently, Liede (1996, 1997a, b; Liede and Meve 1997) has begun to clarify generic circumscriptions within subtribe *Metastelmatinae* Endl. ex Meisn. (*Cynanchinae* K. Schum.; Liede 1997b). Although these circumscriptions currently appear to be somewhat provisional, species of *Metastelma* have stood out as particularly discordant elements within *Cynanchum* sensu Woodson (Liede and Meve 1997) and the recognition of *Metastelma* appears well founded.

In preparing a treatment of *Metastelma* for a revised flora of the Río Mayo region of northwestern México (Levin and Fishbein in Martin et al. 1998), we found it necessary to provide a single transfer from *Cynanchum* to *Metastelma*. Originally, the specimens in question were identified as *Cynanchum wigginsii* Shinnery (Van Devender et al. 1995). Close study of many herbarium collections of *C. wigginsii* [= *Basistelma angustifolium* (Torr.) Bartlett] and the clearly related *Basistelma mexicanum* (Brandege) Bartlett (including the types of both species) revealed that the collections from southeastern Sonora were also similar to the type of *B. mexicanum*. The close relationship of specimens assigned to these taxa was first noted by Bartlett (1909), who erected the genus *Basistelma* to accommodate them as two species. The similarities between the types (and among all collections examined) suggested to us that only a single species was represented. We found that the slight morphological differences in staminal and stylar characteristics noted by Bartlett (1909) and Standley (1924) are variable within small geographic areas (sometimes from the same locality) and that the states of these characters do not covary consistently among herbarium specimens. Thus, we make the following new combination and recognize a new synonym (herbarium acronyms follow Holmgren et al. [1990] and updates).

Metastelma mexicanum (Brandegee) Fishbein & R. Levin comb. nov.—*Melinia mexicana* Brandegee, Zoe 5:216. 1905.—*Basistelma mexicanum* (Brandegee) Bartlett, Proceedings of the American Academy of Arts and Sciences 44:632. 1909.—TYPE: MEXICO, Sinaloa, about 30 mi. east of Culiacan, near Durango border, Cerro Colorado, 1904, *T. S. Brandegee s.n.* (GH!).

Metastelma angustifolium Torr., Report on the U.S. and Mexican Boundary Survey 2:159. 1859, non Turcz., Bjulleten' Moskovskogo Občšestva Ispytatelej Prirody. Otdel Biologičeskij 1852: 315. 1852.—*Melinia angustifolia* (Torr.) A. Gray, Proceedings of the American Academy of Arts and Sciences 12:73. 1877.—*Pattalias angustifolius* (Torr.) S. Watson, Proceedings of the American Academy of Arts and Sciences 24:60. 1889.—*Cynanchum wigginsii* Shinnars, Sida 1:365. 1964.—TYPE: MEXICO, Sonora: Santa Cruz, 1851, *C. Wright 1677* (GH, 3 sheets!, US!).

Metastelma mexicanum grows at the upper elevational limit of tropical deciduous forest and in oak-dominated grassland and woodland in southern Arizona, Sonora, and Sinaloa (Fig. 1). Although it has not yet been collected there, the species is very likely to occur in similar habitats in contiguous southwestern Chihuahua—in the upper watersheds of the Río Yaqui, the Río Mayo, and the Río Fuerte—and perhaps also in northwestern Durango. Like many other members of the genus, it twines on the branches of shrubs and small trees, and upon itself, forming dense tangles under favorable conditions. It is apparently never common; often only a single (occasionally quite robust) individual can be found at any one location (M. Fishbein, personal observation).

Additional specimens examined. MEXICO, Sonora: near Magdalena, 2 Oct 1976, *T. R. Van Devender s.n.* (ARIZ), Jul 1977, *T. R. Van Devender s.n.* (ARIZ), 3 Oct 1982, *G. Starr 180* (ARIZ, CAS), 14 Aug 1983, *T. R. Van Devender s.n.* (ARIZ); Rancho Santa Barbara, 3 Jun 1993, *P. Jenkins 93-88* (ARIZ, MEXU, MO, UCR, USON); Sierra de Alamos, 19 Aug 1992, *V. W. Steinmann s.n.* (ARIZ); Sierra Saguaribo, Aug 1935, *F. Pennell 19,530* (US), 23 Aug 1993, *M. Fishbein 1362* (ARIZ, MO), 24 Aug 1993, *M. Fishbein 1448* (ARIZ). UNITED STATES, Arizona: Cochise Co.: Mule Mountains, 19 Sep 1961, *L. N. Goodding 299-61* (ARIZ), 302-61 (ARIZ), 14 Oct 1961, *L. N. Goodding 439-61* (ARIZ), 5 Sep 1973, *T. R. Wentworth 2211* (ARIZ). Santa Cruz Co.: Canelo Hills, Middle Canyon, 19 Sep 1993, *M. Fishbein 1500* (ARIZ); Pajarito Mountains, Sycamore Canyon, Sep 1976, *J. Kaiser 914* (ARIZ), 13 Aug 1978, *L. J. Toolin 20* (ARIZ), 7 Oct 1981, *T. R. Van Devender s.n.* (ARIZ), 1 Sep 1987, *T. R. Van Devender 87-241* (ARIZ); Patagonia

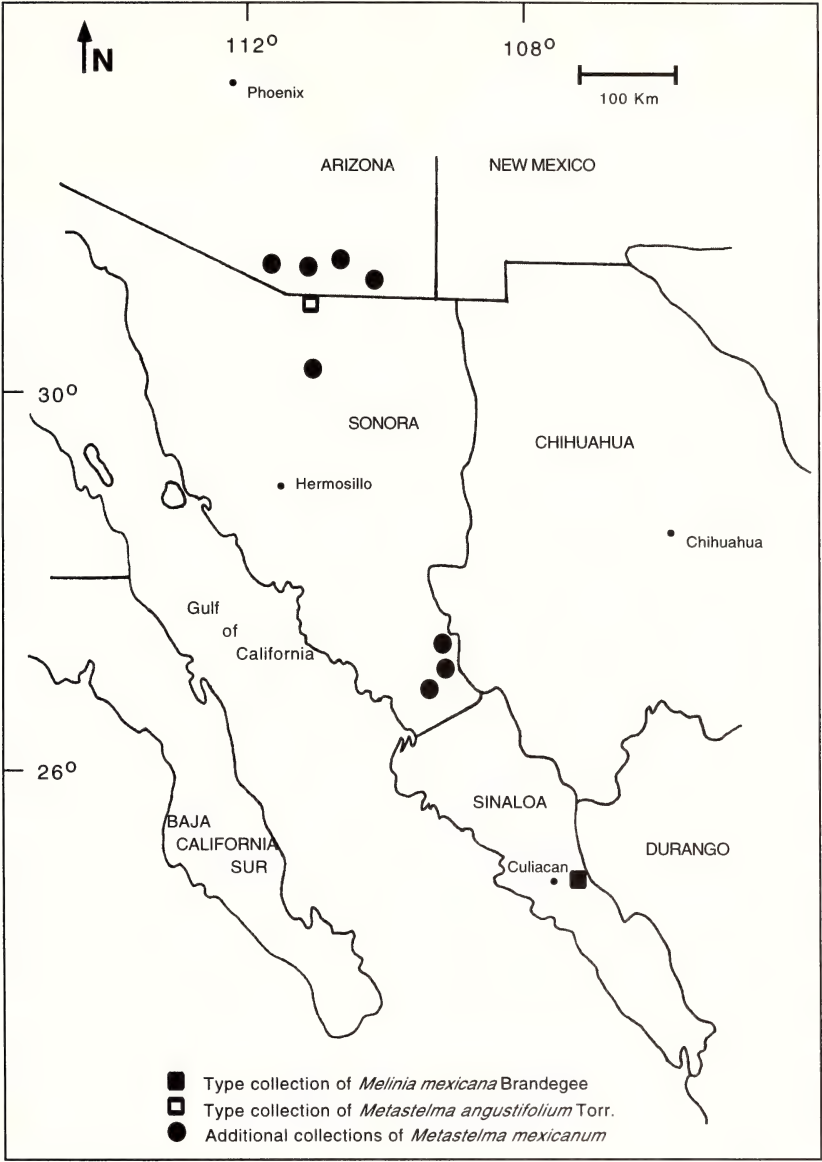


FIG. 1. Known collection localities of *Metastelma mexicanum* in Arizona, U.S., and Sonora and Sinaloa, México. Collection sites within ca. 25 km are represented by a single symbol. Localities of type specimens pertaining to this species are indicated by squares; all other localities are indicated by ovals.

Mountains, 11 Sep 1978, *S. P. McLaughlin 1848* (ARIZ); east of Ruby, 19 Nov 1981, *T. R. Van Devender s.n.* (ARIZ).

Although the earliest epithet applied to this species was *Metastelma angustifolium* Torr., this name was invalid upon publication as a homonym of the slightly earlier *M. angustifolium* Turcz. The earliest validly published basionym pertaining to this species is *Melinia mexicana* Brandege. (*Melinia* Decne. is now considered to be a relatively distantly related genus in subtribe Oxypetalinae K. Schum. [Liede 1997b].) This species was transferred to *Basistelma* by Bartlett (1909), but has never been assigned to *Metastelma*, necessitating the transfer made here.

Recent treatments of *Metastelma mexicanum* either maintain *Basistelma* as a genus or include *Metastelma* and *Basistelma* in a greatly expanded *Cynanchum*. Kearney and Peebles (1951) recognized *Metastelma* (*M. arizonicum*) and *Basistelma* (*B. angustifolium*) in Arizona. Following Woodson's (1941) concept of an inclusive *Cynanchum*, Shinnars (1964) made several transfers from *Metastelma* to *Cynanchum* and also transferred *Basistelma angustifolium* (proposing the nomen novum, *Cynanchum wigginsii*). This generic concept was followed in the most recent treatment of Arizona plants (Sundell 1994). Recently, Liede (1997a, b) assigned taxa referable to *Metastelma mexicanum* to two different genera (see below, "The status of *Metastelma*").

THE STATUS OF *BASISTELMA*

Basistelma was segregated from *Metastelma* by Bartlett (1909) and Standley (1924) primarily on the basis of the elongate style apex of the two species here considered to be conspecific. However, this character is found in some individuals of *Metastelma arizonicum* A. Gray from the Sonoran Desert, and even in other distantly related asclepiadaceous genera, as in *Matelea cordifolia* (A. Gray) Woodson (M. Fishbein and R. Levin, personal observation). Standley (1924) also contrasted the valvate aestivation of the corolla lobes in bud of *Metastelma* with the contorted, imbricate aestivation of *Basistelma* and *Cynanchum*. However, we have found contorted, imbricate aestivation in some species included in *Metastelma* by Standley (1924), e.g., *M. arizonicum* A. Gray (as *M. watsonianum* Standl.), *M. barbigerrum* Scheele, *M. palmeri* S. Watson, and *M. pringlei* A. Gray. Thus, the few characteristics previously used to separate *Basistelma* from *Metastelma* are inadequate and obscure the close relationship among species of these genera. Recognizing *Basistelma* would almost certainly create a paraphyletic *Metastelma*.

THE STATUS OF *METASTELMA*

Liede (1997a) discussed the circumscription and distinguishing features of *Cynanchum* and related genera that occur in the Amer-

icas. Species of *Metastelma* are most similar to those of *Ditassa* R. Br., *Orthosia* Decne., *Tassadia* Decne., and *Cynanchum* sect. *Macbridea* (Raf.) Liede and sect. *Microphyllum* Liede. Compared to other sections of *Cynanchum* and the other genera of Metastelmatinae (Liede 1996, 1997a), these taxa share many characteristics with *Metastelma* (e.g., delicate twining stems; small, relatively narrow leaves that are never deeply cordate at the base; and minute flowers produced in contracted "umbellate" inflorescence units [sensu Fishbein and Venable 1996]). Distinguishing characteristics of these taxa are conveniently summarized by Liede (1997a, Table 1). The most reliable character to differentiate species of *Metastelma* from those of similar taxa, as circumscribed by Liede (1997a), is the composition of the corona. Species of *Metastelma* and *Ditassa* are distinguished from those of related genera by possessing unfused corona segments located only opposite the stamens; in other similar genera, species possess coronas of fused segments positioned both opposite and alternate the stamens (coronas are absent in some species of *Cynanchum* sect. *Macbridea*). Species of these two genera are also the only ones in this group of taxa that possess long, dense, adaxial trichomes of the corolla lobes. *Metastelma* and *Ditassa* (which are strictly South American) are distinguished from each other by the adaxial appendage of the corona segments found only in species of *Ditassa*.

Other characteristics of *Metastelma* appear to be less reliable for distinguishing these species from those of related genera. Liede (1997a, Liede and Meve 1997) suggested that the presence of the distinctive corolline trichomes noted above is the most reliable distinguishing character of *Metastelma*. However, we have found only minute corolline trichomes or papillae in several species in North America that we consider to be unambiguous members of *Metastelma* (e.g., *M. cuneatum* Brandegees, *M. palmeri* A. Gray) and species of *Ditassa* share possession of these trichomes, as noted above (Liede 1997a, Table 1). Liede (1997a, Table 1) also suggested that species of *Metastelma* can be distinguished from most species of *Cynanchum* by the regular production of two fruits (versus one) per flower; however, this characteristic appears to be exceedingly rare in all species of *Metastelma* in North America that we have studied, based on examination of plants in the field and numerous herbarium specimens.

Although the species of *Metastelma* are distinguished from those of similar genera by subtle characteristics, we concur with Liede (1997; Liede and Meve 1997) that the distinctive corona morphology merits generic recognition. Although it is possible that a broadly circumscribed *Cynanchum* may be monophyletic with *Metastelma* (and related genera, e.g., *Ditassa*) nested within (essentially Woodson's [1941] position), recent progress in the systematics of *Cynan-*

chum s.l. suggests the polyphyly of a taxon circumscribed so broadly (Liede 1996). A better case could be made for combining *Metastelma* and *Ditassa*, but, to our knowledge, this generic concept has not been proposed. Unfortunately, simultaneous phylogenetic study of all relevant taxa has not been attempted as yet. Based on existing evidence, recognition of *Metastelma* is warranted.

Surprisingly, Liede (1997b) treated *Basistelma* as a synonym of *Cynanchum*, despite the corona morphology (i.e., unfused segments opposite the stamens) of *Metastelma mexicanum*, which is diagnostic of *Metastelma*. However, Liede (1997a) also placed *C. wigginsii*, inexplicably, in synonymy with *Orthosia kunthii* Decne. (*Cynanchum kunthii* [Decne.] Standl., *Metastelma angustifolium* Turcz.). Species of *Orthosia* were recognized as distinct from those of *Cynanchum* by Liede (1997a) based on the apically dentate or toothed, fused corona segments of *Orthosia* (however, the segments of *O. kunthii* are untoothed [M. Fishbein, personal observation]). Regardless of the correct generic assignment of *O. kunthii*, *M. mexicanum* is clearly not conspecific; specimens that we have identified as *O. kunthii* (we have not seen the type) possess much smaller corollas with shorter, adaxially glabrous lobes, and corona segments that are fused basally. Specimens of *Metastelma mexicanum* possess all of the diagnostic features of *Metastelma*, as noted above, including long, dense adaxial trichomes on the corolla lobes and unfused corona segments opposite the stamens. When identified using Liede's (1997a) key to New World sections of *Cynanchum* and related genera, they are unambiguously assigned to *Metastelma*.

INTRASPECIFIC VARIATION IN *METASTELMA MEXICANUM*

We initially attempted to recognize the southern and northern populations corresponding to *Basistelma mexicanum* and *B. angustifolium* of Bartlett (1909) as distinct subspecies of *Metastelma mexicanum*, but this treatment appears untenable. These entities were distinguished as species by Bartlett (1909) as follows: *B. mexicanum* was said to differ by possessing a shorter style apex, "more fleshy" corona segments, and more recurved apical anther appendages. However, corona segments appear to be uniformly laminate in all specimens that we have examined. It is noteworthy that Standley (1924) omitted this distinguishing character in his treatment. We have found the other two characters to be variable within populations (i.e., herbarium specimens from the same, precise locality) and to not covary consistently. Long and short style apices are present in both northern and southern populations. Apical anther appendages differ more consistently between northern and southern populations than the length of the style apex: those on plants from Arizona and northern Sonora are typically erect or nearly so, whereas those on

plants from southern Sonora and Sinaloa may be erect, but more commonly have recurved tips. We consider this slight and inconstant distinction insufficient for recognition of infraspecific taxa.

CONCLUSION

Metastelma mexicanum is easily distinguished from other species in the genus in North America, as circumscribed by Liede (1997a). The exceedingly narrow, almost filiform leaves are unlike those of any other species in North America, and the elongate style apex is shared only with some plants of *M. arizonicum*. The combination of these two characteristics, in addition to the unique, erect, apical anther appendages, serves to distinguish *M. mexicanum* from other species of *Metastelma* in North America.

Metastelma mexicanum is as yet a poorly known species. We examined all specimens collected in México housed at the cited herbaria and all specimens collected in Arizona housed at ARIZ. The species appears to rare throughout its range (Fishbein and Warren 1994; Levin and Fishbein in Martin et al. 1998). Further collecting on the Pacific slope of the northern Sierra Madre and in the mountains of northeastern Sonora is required to definitively evaluate previously hypothesized patterns of morphological variation within this species. Proposed relationships between *M. mexicanum* and other species of *Metastelma* would be highly speculative at this time. The genus is badly in need of both monographic and phylogenetic study.

ACKNOWLEDGMENTS

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**ATRIPLEX PACHYPODA (CHENOPODIACEAE), A NEW
SPECIES FROM SOUTHWESTERN COLORADO AND
NORTHWESTERN NEW MEXICO**

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ABSTRACT

Atriplex pachypoda is a newly described annual species from southwestern Colorado and northwestern New Mexico. It occurs in alkaline seepage areas and adjacent disturbed slopes in La Plata county, Colorado, and Rio Arriba county, New Mexico. It is morphologically most similar to *A. caput-medusae* Eastwood, but differs in its smaller, more spreading habit, narrow-ovate to ovate-elliptical instead of deltoid-ovate leaves, flattened instead of uncompressed fruiting-bracts, small, cone-shaped, instead of large, flattened, fruiting-bract appendages, larger, central, marginal tooth of fruiting-bract, more stout fruiting-bract pedicel, and later flowering- and fruiting-periods.

This somewhat obscure annual species was first found 14 Aug 1991 at the south edge of Dulce, Rio Arriba County, New Mexico. Only two other populations have been found, one at the southwest edge of Bayfield, La Plata County, Colorado, the other in Dry Creek, north of highway 140, about 7 km west of Bayfield.

Atriplex pachypoda Stutz & Chu, sp. nov. (Fig. 1)—TYPE: USA, Colorado, La Plata Co., Dry Creek, ca. 7 km W of Bayfield, T34N R7W S12, 21 Sep 1995, *H. C. Stutz* 9822 (holotype, BRY).

Herba annua, 10–20 cm alta. Caulis erectus, ramosus; basales rami oblique ascendentes vel decumbentes, fere centrale caule aequilongi, tetragoni vel fere sic, plerumque leviter purpureorubelli, sparse furfuracei. Folia Kranz-typorum anatomiis, petiolata; lamina angusti-ovata, usque ovato-elliptica, 1–1.5 cm longa, 0.5–1 cm lata, apice obtusa vel breviter acuminata, basi cuneata, margine integra, costa conspicua, utrinque dense furfuracea, cinereo-viridis; petiolus 2–5 mm longas. Staminates et pistillati flores mixti in glomerulos, axillares ad totos ramos; perianthium staminalis floris globosum, ca. 1 mm diam. 4–5-partium; segmenta elliptica, apice leviter cucullata, membranacea, secus costam leviter carnosa et viridia; stamina 4–5, antheris ca. 0.3 mm longis, filamentis filiformibus ca. 0.5 mm longis. Fructiferae bracteae transverso-oblongae, compressae, 4–5 mm lon-

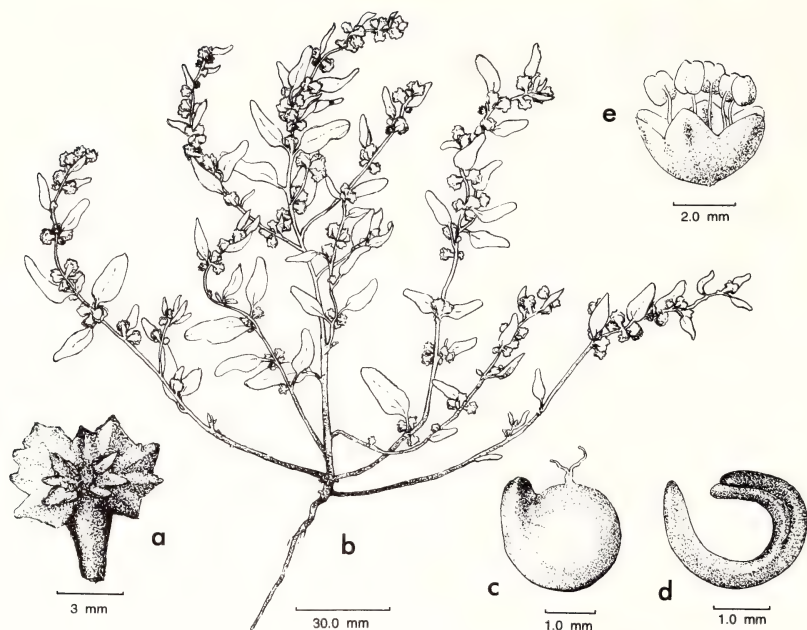


FIG. 1. *Atriplex pachypoda*. a. Fruiting bract. b. Habit. c. Utricle. d. Embryo. e. Male flower. (Drawings by Marcus Vincent).

gae, 4–5 mm latae, margine irregulariter serratae, medio dente quam 2 contigui laterales dentes flerumque leviter minori, utrinque saepe aliquot irregulibus corniculatis appendicibus; stipes fructiferae bractae validus, 2–3.5 mm longus, 1–2 mm diam. Utriculus ovatus, membranceo pericarpio. Semen flavo-brunnolum, ca. 2 mm latum, perispermio farinaceo; radicula supera. Chromosotum numerus $2n=18$.

Proxima *Atriplex caput-medusae* Eastwood, quae differt folius deltato-ovatus usque rhomboideo-ovalis; fructiferis bracteis margine partitis.

Annual herb, 10–20 cm tall. Stem ascending, much branched, basal branches oblique, mostly decumbent, nearly as long as central stem, tetragonous or nearly so, usually slightly purple-reddish, sparsely furfuraceous. Leaves petiolate, petiole 2–5 mm long; blades narrow-ovate to ovate-elliptical, 1–1.5 cm long, 0.5–1 cm wide, apex obtuse or acuminate, base cuneate, entire, midrib conspicuous, densely furfuraceous on both surfaces, grey-green in color; Kranz-type anatomy. Male and female flowers in mixed glomerules, axillary throughout all branches; perianth of staminate flower depressed, globose, ca. 1 mm in diam., 4–5-parted; segments elliptical, slightly

hooded at apex, membranaceous, midrib slightly fleshy, green; stamens as many as perianth segments, anthers ca. 0.3 mm long, filaments ca. 0.5 mm long; rudimentary pistil present, punctiform. Fruiting bracts transverse-oblong in outline, 3.5–4 mm long, 4–5 mm wide, depressed, with stout, short stalk; margins irregularly denticulate, each marginal tooth with prominent vein to apex, middle tooth equal to, or slightly smaller than 2 contiguous teeth; usually with several irregular cone-shaped appendages on each surface; stalk of fruiting bracts 2–3.5 mm long, 1–2 mm wide. Utricle ovate, with membranaceous pericarp. Seed yellow-brown, ca. 2 mm broad; perisperm farinaceous; radicle superior. Flowering and fruiting period: August–October. Chromosome number: $2n=18$ (determined from aceto-carmines squashes of pollen mother-cells derived from anthers of staminate flowers fixed and stored in 5% acetic acid).

Paratypes. USA, Colorado: La Plata Co., Bayfield, T34N R7W S10, 3 Sep 1992, *H. C. Stutz* 95696 (BRY); Bayfield, 17 Sep 1993, *H. C. Stutz* 95937 (BRY); Dry Creek, 4 mi W of Bayfield, T34N R7W S12, 2 Oct 1993, *H. C. Stutz* 95954 (BRY); SW side of Bayfield, 19 Oct 1993, *H. C. Stutz* 95970 (BRY); Bayfield, 18 Aug 1994, *H. C. Stutz* 9663 (BRY); Dry Creek, 15 mi E of Durango, 16 Aug 1995, *H. C. Stutz* 9806 (BRY). New Mexico: Rio Arriba Co., Dulce, S edge of town, T31N R2W S35, abundant, 14 Aug 1991, *H. C. Stutz* 95586 (BRY); Dulce, S edge of town, scarce, 8 Sep 1994, *H. C. Stutz* 9667 (BRY).

Taxonomic relationships. *Atriplex pachypoda* appears to be most closely related to *A. caput-medusae* but differs in several significant characteristics including smaller stature (10–20 cm vs. 20–30 cm), narrow-ovate to ovate-elliptical leaves (5–10 mm wide, 10–15 mm long), instead of rhomboid-ovate to deltoid-ovate leaves (15–20 mm wide, 10–25 mm long) (Fig. 2) and flattened instead of uncompressed fruiting-bracts (Fig. 2). Fruiting-bracts of *A. pachypoda* have dentate margins and a few lateral cone-shaped appendages, whereas fruiting-bracts of *A. caput-medusae* have irregularly parted margins and bear numerous lateral, flattened appendages (Fig. 2). The central marginal tooth of *A. pachypoda* is nearly as large as the contiguous marginal teeth whereas, in *A. caput-medusae*, the central tooth is minute and obscured by much larger contiguous teeth. Both *A. pachypoda* and *A. caput-medusae* have fruits with conspicuous pedicels, but pedicels of *A. caput-medusae* are elongate (5–6 mm) and narrow, tapering from ca. ½ mm to ca. 1 mm in diameter whereas those of *A. pachypoda* are shorter (2–4 mm), and more massive, tapering from ca. 1.5 mm to ca. 2.0 mm (Fig. 2). Anthesis in *A. caput-medusae* is in early spring (May–June); anthesis in *A. pachypoda* is in late summer (August–October). Both *A. pachypoda* and *A. caput-medusae* are diploids ($2n=18$) (determined from aceto-car-

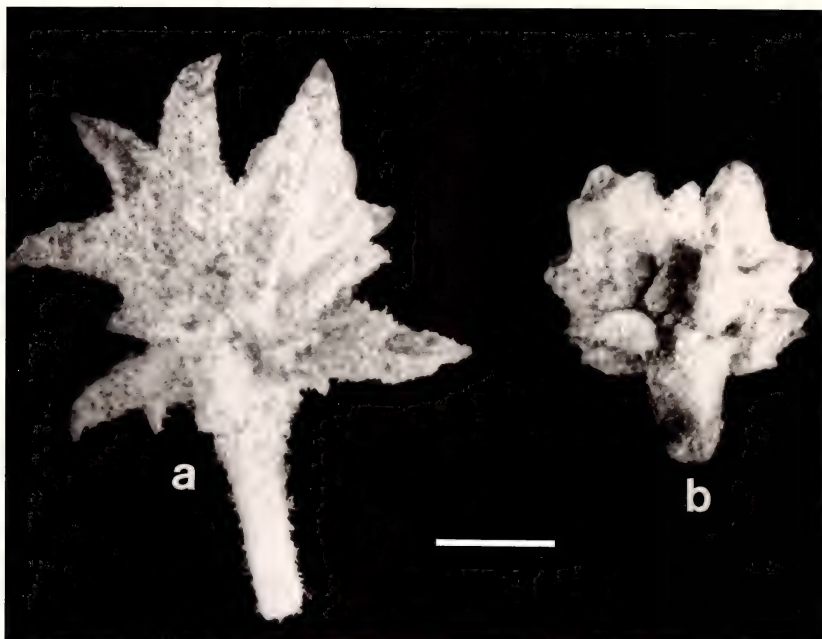


FIG. 2. Fruiting bracts of *Atriplex caput-medusae* (left) and *A. pachypoda* (right). Bar = 3 mm.

mine squashes of pollen-mother-cells taken from anthers fixed and stored in 5% acetic acid).

Distribution and habitat. *Atriplex pachypoda* has been found in only three localities: southwest side of Bayfield, LaPlata county, Colorado, along Dry Creek, about 7 km west of Bayfield, and at the south outskirts of Dulce, Rio Arriba county, New Mexico. Several intensive searches have been made throughout southwestern Colorado and northwestern New Mexico but no other populations have yet been found. However, because plants were abundant in the population at Dulce, New Mexico, in 1991 but scarce or absent in 1993 and were sometimes abundant and at other times scarce, at Bayfield, Colorado, other populations may yet be found when climatic conditions are favorable for their growth.

The three known populations of *A. pachypoda* are in raised areas near alkaline seepage areas. No *A. pachypoda* plants were found in the wet bottoms of these seepage areas but were plentiful on slightly elevated terrain within the seepages, and on the shoulders of nearby roadcuts.

Associated species. *Atriplex pachypoda* sometimes occurs in small, pure stands usually covering areas of less than 5.0 m² with

no other associated species but is often accompanied by plants of *Atriplex powelli* Watson, *A. subspicata* Rydberg, *A. heterosperma* Bunge, *Chrysothamnus nauseosus* (Pallas) Britt, *Distichlis spicata* (L.) Greene and *Polygonum* sp.

Phenology. Flowering and fruiting is mostly in late summer (August–October). Plants of *A. pachypoda* and *A. caput-medusae* grown in greenhouses and nurseries at Brigham Young University, Provo, Utah, from seed collected from plants growing in natural populations showed the same distinctive attributes expressed by plants growing in nature, indicating high heritability of these characteristics.

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NOTEWORTHY COLLECTIONS

BRITISH COLUMBIA

SILENE SPALDINGII Wats. (CARYOPHYLLACEAE).—Tobacco Plains, vicinity of Roostville, between Davis Rd. and the Canada-U.S. border on Beau West Ranch, UTM 6412 54296, elev 850 m, on disturbed grassland with *Lupinus sericeus*, *Hypericum perforatum*, *Castilleja tenuis*, and *Castilleja thompsonii*, 8 Aug 1995, Michael T. Miller, verified by G. A. Allen (UVIC).

Previous knowledge. This rare campion is known from about 70 localities in Washington, Oregon, Idaho and Montana (B. Heidel, personal communication). The newly reported population (with an estimated minimum size of 100 plants) is 0.6 km N of the U.S. border, and approximately 1.3 km NE of the nearest documented occurrence in Flathead Co., Montana. We thank George Douglas of the B.C. Conservation Data Centre and Bonnie Heidel of the Montana Natural Heritage Program for providing us with information on known and suspected occurrences of this species along the B.C.-Montana border.

Significance. First record for Canada, and the most northerly record for this species. It is not clear whether the new record is the result of recent colonization, or has been overlooked by previous collectors. The locality is approximately 7 km N of the Dancing Prairie preserve in Montana, which harbors probably the largest known population of *S. spaldingii*.

—MICHAEL T. MILLER and GERALDINE A. ALLEN, Department of Biology, University of Victoria, Victoria, British Columbia V8W 3N5, Canada.

A REVISION OF THE GENUS *HESPERALOE* (AGAVACEAE)

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ABSTRACT

Hesperaloe is a North American genus consisting of three described species. Recent exploration of northern Mexico for plants with horticultural possibilities has resulted in the discovery of three new taxa. These are geographically isolated from each other and from the three previously described taxa. Descriptions and illustrations for two new species and one new subspecies are provided. A key to all five species is included.

RESUMEN

Hesperaloe es un género norteamericano que consiste en tres especies ya anteriormente descritas. Recientemente se han descubierto tres nuevas taxa en México norteño en exploraciones para plantas con posibilidades hortícolas. Las nuevas taxa están aisladas geográficamente la una de las otras y de las tres descritas anteriormente. Se encuentran aquí descripciones e ilustraciones de las dos nuevas especies y la nueva subespecie. También se incluye una clave de las cinco especies.

INTRODUCTION

Hesperaloe is a North American genus consisting of six taxa. Four taxa occur on the eastern side of the Sierra Madre Occidental, from Texas to San Luis Potosí, Mexico, while the other two taxa occur on the western side of the Sierra Madre Occidental, in Sonora, Mexico (Fig. 1). The genus was erected by Engelmman in 1871 to accommodate the recently described *Aloe yuccaefolia* A. Gray. However, Torrey (1859) had previously described *Yucca parviflora* which, according to Coulter (1894) included the taxon then known as *Hesperaloe yuccaefolia* Engelmman. The combination became *Hesperaloe parviflora*. (Torrey) Coulter.

In 1862, Koch described *Yucca funifera* which Trelease (1902) decided fit better in *Hesperaloe* and made the combination *Hesperaloe funifera* (Koch) Trelease. It was not until 1967 that another species of *Hesperaloe* was discovered, when Gentry (1967) described *Hesperaloe nocturna* from Sonora. Although flowers of *H. funifera* and *H. nocturna* are similar, plants are distinct vegetatively, separated geographically by about 750 km, and occur on opposite sides of the Sierra Madre Occidental. Engard (personal communication) proposed the name *Hesperaloe chiangii* for plants growing in San Luis Potosí. His life was cut short before he could continue his proposed work on the genus. After examining a specimen growing in his yard, I pursued this taxonomic question. Prior to my ar-

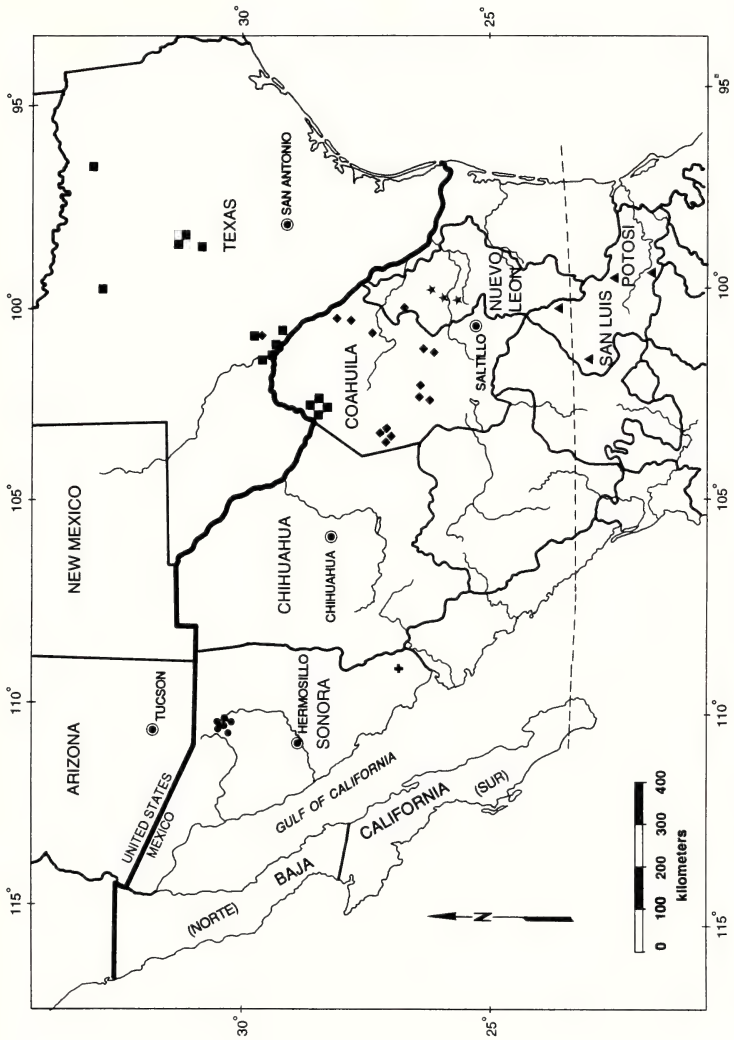


FIG. 1. Distribution of *Hesperaloe*. ★ = *H. campanulata*, ◆ = *H. funifera* ssp. *funifera*, ▲ = *H. funifera* ssp. *chiangii*, ● = *H. nocturna*, ■ = *H. parviflora*, and + = *H. tenuifolia*.

ranging a collecting trip to San Luis Potosí, two other undescribed taxa were found in two widely separated localities, one occurring in central Nuevo León, Mexico, the other in southern Sonora, Mexico. In light of these developments, it became apparent that a revision of the genus *Hesperaloe* was needed. The present revision is based on field and horticultural work with all taxa.

SYSTEMATIC TREATMENT

HESPERALOE: Engelmann in King, Geological Exploration of the 40th Parallel. 5:497. 1871.

Short- to long-rhizomatous perennials with stemless rosettes of leaves either tightly packed or widely separated and forming large rings. Main roots thick and fleshy, with many fibrous feeder roots. Leaves few to many, either thin, narrow, and arching to recurved or thick, broad, and stiffly erect, canaliculate; margins brown or white; marginal fibers thin and tightly curled to thick and nearly straight, white or gray. Flowering stalk terminal from the center of mature rosettes, ascending, to 4 m tall, racemose or paniculate with 3–8 lateral side branches in the upper one-half. Flowers on indeterminate lateral spurs, either on main stalk or side branches. Flower color combination of green, white, and purplish-brown to red, pink, salmon, or coral to rarely yellow. Corolla shape tubular to narrowly to broadly campanulate or rotate-campanulate. Stamens included to exserted. Fruit a woody, dehiscent capsule, beaked or not, transversely rugose, persistent. Seeds large, black, flat, and thin.

KEY TO THE SPECIES

1. Tepals white with greenish purple midstripe, reflexed at anthesis.
 2. Leaves spreading to arching, 1–1.5 m long, maximum width 1–2 cm wide, marginal fibers fine 3. *H. nocturna*
 - 2' Leaves stiff and erect, 1–2 m long, maximum width 2–6 cm, marginal fibers coarse.
 3. Rhizomes short, <30 cm; leaves ≤1.5 cm thick at base; marginal fibers ≤1 mm diameter; plants from Coahuila and Nuevo Leon 2a. *H. funifera* ssp. *funifera*
 - 3' Rhizomes long, >30 cm; leaves >1.5 cm thick at base; marginal fibers 2–3 mm diameter; plants from San Luis Potosí. 2b. *H. funifera* ssp. *chiangii*
- 1' Tepals pink, red, or coral, reflexed or straight, forming a tube.
 4. Leaves thin and flexible, spreading, 0.5–1.0 m long, maximum width 5–8 mm wide; flowers rotate; tepals pinkish-red, reflexed, to 13 mm long; fruits globose, beakless or with a beak ≤1 mm long. 5. *H. tenuifolia*
 - 4' Leaves stiff, upright to spreading, more than 8 mm wide; flowers tubular to campanulate; tepals longer than 15 mm; fruits with beak >4 mm long.
 5. Leaves dark green, recurved and twisting, deeply canaliculate, 30–60(120) cm long, less than 15 mm wide; flowers tubular; seeds 9–10 mm long, 6–7 mm wide 4. *H. parviflora*
 - 5' Leaves medium green, erect to spreading, not deeply canaliculate;

60–105 cm long, 15–26 mm wide flowers tubular-campanulate to campanulate; seeds 6–9 mm long, 5–6 mm wide.
 1. *H. campanulata*

1. ***Hesperaloe campanulata*** G. D. Starr, sp. nov. (Fig. 2)—TYPE: USA, Arizona: (MEXICO, Nuevo León 550 m, 26°13'N, 100°7'30"W) Grown in author's garden in Tucson from an offset collected 11 Nov 1989 at Mamulique micro-ondas; *Starr 93-001* (holotype: ARIZ!; isotypes: TEX!, MO!, MEXU!).

Planta acaulis, cespitosa, 0.6–1 m lata; foliis lineareo-lanceolatus, 60–105 cm longis, 1.5–1.6 cm latis, margine angusto sparse filifero; inflorescentia simplici paniculata, 3 metralis; flores pedicillati, tepala roseus margine albus 18–22 mm longa, 4–8 mm lata; capsulae globosae 2–3 cm longae, 2–2.5 cm latae; semina nigra 6–9 mm longa, 5–6 mm lata.

Plants acaulescent, forming moderately caespitose clumps to 0.6–1 m across. Leaves stiff and erect to slightly spreading, canaliculate, linear-lanceolate, 60–105 cm long, 15–26 mm wide at widest point (one-third from base) tapering to tip, medium green, margins finely filiferous. Inflorescence 3 m long, raceme or panicle with 2–5 branches in upper one-third. Flowers tubular-campanulate to broadly campanulate; pedicels 8–13 mm long; outer tepals linear to linear-lanceolate, adaxial face white, abaxial face pink with broad, white margins, 18–22 mm long, 4–8 mm wide; stamens and pistill included; filaments 14–15 mm long, adnate to tepal base for 3 mm; anther sacs 3 mm long; ovary 6 mm long, 4 mm wide at anthesis, style 9–13 mm long. Capsules globose or oblong, 2–3 cm long (excluding beak) 2–2.5 cm wide, beak 4–11 mm long; seeds black, 6–9 mm long, 5–6 mm wide.

Paratypes. MEXICO, Nuevo León; 13 miles N of Sabinas Hidalgo, Mexico highway 85, 400 m, 26°38'N, 100°01'W 15 Aug 1990 *Starr 90-001* (ARIZ); 35 miles N of Sabinas Hidalgo on Mexico highway 85, 100 m, 26°52'N, 99°49'30"W, 16 May 1991, *Starr 91-001* (ARIZ).

Phenology and distribution (Fig. 1). Flower spikes begin to appear in late March or early April with flowering extending into October. Flowers open in the evening and are pollinated during the night by bats and hawkmoths. The following day, flowers close some, forming a tube and are visited by hummingbirds. *Hesperaloe campanulata* occurs in open Chihuahuan Desert scrub on limestone slopes and hillsides. Associated species include *Acacia berlandieri*, *Acacia farnesiana*, *Acacia rigidula*, *Bauhinia lunarioides*, *Cassia greggii*, *Cercidium texanum*, *Cordia boissieri*, *Fraxinus greggii*, *Guaiaacum angustifolium*, *Leucophyllum frutescens*, *Vauquelinia angustifolia* var. *heterodon*, and *Yucca rostrata*. The species is known

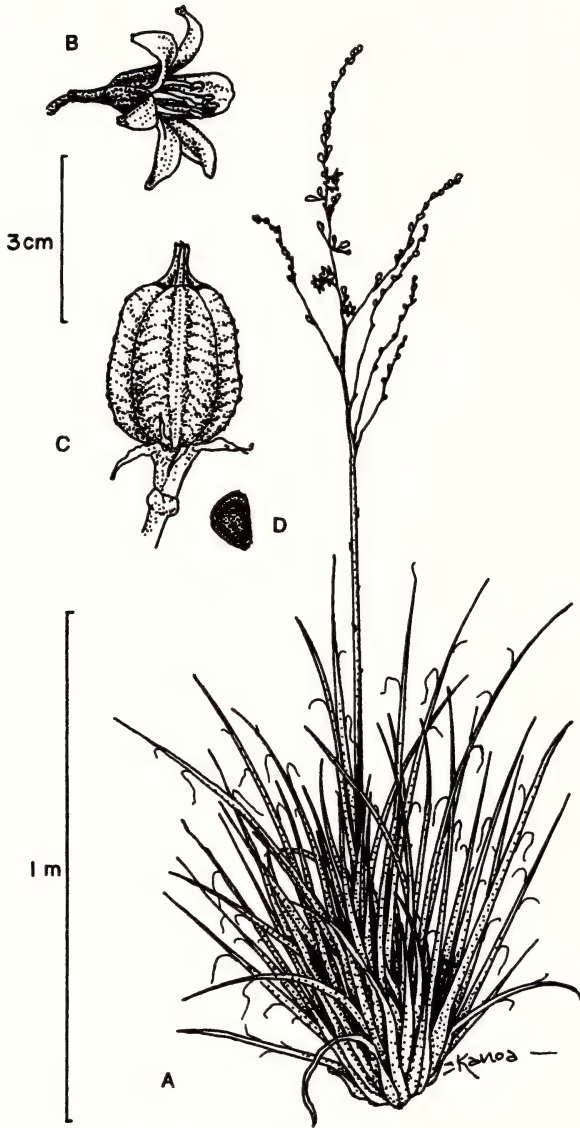


FIG. 2. *Hesperaloe campanulata*. A. Habit. B. Flower. C. Capsule. D. Seed.

only from a limited area in north-central Nuevo León at 500–600 m. Annual precipitation in this limited geographical range varies from 500 to 700 mm.

2. *Hesperaloe funifera* (Koch) Trelease, Annual Report of the Missouri Botanical Garden 13:36. 1902.—*Yucca funifera* Koch, Belgique Horticole 12:132, 1862.—*Agave funifera* Lemaire, L'Illustration Horticole. 11(misc.): 65. 1864.—*Yucca funifera* Lemaire, L'Illustration Horticole. 13:99. 1866.—TYPE: None cited. NEOTYPE (here designated): MEXICO, Coahuila; 4 miles east of Esmeralda Mine along road to Cuatro Ciénegas, 8 May 1973, R. G. Engard and H. S. Gentry 23241 (neotype: ARIZ!).

Hesperaloe davyi Baker, Kew Bulletin of Miscellaneous Information 1898:226.—TYPE: (probably a specimen preserved in K; Baker cited source as plant grown in botanical garden of University of California, Berkeley and sent by J. Burt Davy. (Isotype: UC!))

Plants caespitose, forming clumps up to 1.5 m across, or long rhizomatous and forming fairy rings to 2 m or more in diameter. Leaves stiff and erect, light to dark green or yellowish-green, canaliculate, linear-lanceolate or lanceolate, 1–2 m long, 3–6 cm wide, margins brown, medium to coarsely filiferous with white or gray loosely coiled fibers. Inflorescence a 2–4 m tall panicle with 3–8 branches mostly in upper one-half of stalk. Flowers rotate-campanulate, in indeterminate fascicles; tepals white on adaxial face, 17–20 mm long, abaxial face of inner tepals green and white with a narrow center stripe tinged brownish purple, 8–9 mm wide, abaxial face of outer tepals green at base and reddish purple on upper two-thirds, 6–7 mm wide; stamens and pistil included; ovary at anthesis 10–12 mm long and 4–5 mm wide; pedicel 5–6 mm long. Capsules globose or broadly oblong, 2.5–3.5 cm long 2.5–3.5 cm wide, sharply beaked, beak 2–4 mm long; seeds 8–9 mm long, 5–7 mm wide, black.

In 1862, Koch gave a minimal description of *Yucca funifera* from material given to him by Jean Verschaffelt, a collector of plants for horticulture. There was no type designated and there are no known existing specimens that were used by Koch. Lemaire (1864), without mentioning either Koch or Verschaffelt, described *Agave funifera* from material introduced from Mexico by the Tonel Brothers. Again there was no type specimen designated and there are no known existing specimens. Then in 1866, Lemaire in his treatise on *Yucca* wrote that he mislaid the documents concerning this species, and proceeded to give a brief description of *Yucca funifera*. Apparently Lemaire changed his mind on the correct placement of the species, but still did not designate a type specimen. *Hesperaloe davyi* was named by Baker (1898) from material sent to him by Davy. Baker stated that the material he received from Davy was from the garden

at the University of California at Berkeley. Although he did not designate a type, Baker's description fits that of *Hesperaloe funifera*. In 1902, Trelease mentioned that Davy told him (Trelease) that there was no record of the source of the seeds from which the plant Baker used for his description was grown. However, he went on to say that Franceschi of Santa Barbara stated that two original plants were raised, with one flowering in 1898, providing the material for which Baker based his description. Franceschi sent suckers from the other plant to Kew and to the Missouri Botanical Garden. Trelease (1902) listed *Hesperaloe engelmannii* Baillon and *H. engelmannii* Urbina as synonyms for *H. funifera*. However, the references are simply catalog listings and were not nomenclatural acts by either author. Both references are based on Pringle's number 3911 from Hacienda de la Angostura which was originally misidentified. *Hesperaloe engelmannii* was a name used by Krauskopf for plants he collected along the western branch of the Nueces River. Krauskopf described these as having reddish petals that is indicative of *Hesperaloe parviflora*, not *H. funifera*. Therefore, the references to *Hesperaloe engelmannii* as a synonym of *Hesperaloe funifera* are incorrect. Trelease (1902) was the first to make reference to an actual specimen that was collected and deposited in a herbarium. He stated that the Engelmann herbarium (now at MO) contained a specimen collected by Wislizenus in 1847 at Cerralvo northeast of Monterey. He also mentioned capsules collected by Parry in 1878 from "the plains between Monterey and the Rio Grande" as being similar to those collected by Wislizenus. Trelease (1902) mentioned a third specimen that was collected by Wood in 1900 in the state of Nuevo León that is in the herbarium of the Field Columbian Museum. None of these three specimens represent type material and a neotype is hereby designated.

2a. *Hesperaloe funifera* (Koch) Trelease subsp. *funifera*.

Plants caespitose, forming clumps up to 1.5 m across. Leaves stiff, erect, light green or yellowish-green, canaliculate, linear-lanceolate or lanceolate, 1–2 m long, 3–4 cm wide (when flattened) from base to middle, tapering from middle to apex, margins brown, with 1 mm thick, white or gray loosely coiled fibers.

Phenology and distribution (Fig. 1). Inflorescences begin showing in spring with flowers appearing from April through August or September. This subspecies occurs in central and northeastern Coahuila and one locality in western Nuevo León at elevations of 500–1000 m. Average annual precipitation ranges from 100 to nearly 500 mm. Associated plants include *Acacia rigidula*, *Agave lechuguilla*, *Cordia boissieri*, *Larrea divaricata*, *Leucophyllum frutescens*, *Opuntia leptocaulis*, and *Prosopis glandulosa*. There is an unusual popula-

tion that occurs within a five mile stretch along Nuevo León Highway 1. All plants have leaves about 1 m long. Some plants have typical *H. funifera* flowers while others have flowers more campanulate-rotate with tepals flushed pinkish-red along the margin.

Specimens examined. MEXICO, Coahuila; 23 miles SW of Allende, 1 May 1959, *D. S. Correll and I. M. Johnston* 21277 (LL); Peyotes (Kilometer 88), 27 Apr 1900. *Trelease* (MO); 63 miles S of Piedras Negras on Mexico Highway 57, 17 Aug 1971, *L. McGill, B. Parfitt, and D. Keil* 7841 (ARIZ); on desert near Rancho Santa Teresa S of Castaños, 19 Jun 1936, *F. L. Wynd and C. H. Mueller* 187 (ARIZ); 11–12 miles SW of Cuatro Cienegas on road to San Pedro, 15 Oct 1972, *R. G. Engard and H. S. Gentry* 23138 (ARIZ); 2.5 miles E of Esmeralda on road to Est. del Oro, N of Sierra Mojada, 27°16'N, 103°38'W, 20 Sep 1972, *J. Henrickson* 7830 (ARIZ); 3–4 miles N of San Lazarus on highway to Monclova, 9 Oct 1972, *R. G. Engard and H. S. Gentry* 23108 (ARIZ). Nuevo León; Rancho Resendez, Lampazos, 24 Jun 1937, *M. T. Edwards* 341 (ARIZ); 3.9 miles S of Lampazos on Mexico Highway 1, 15 Aug 1990, *G. Starr s.n.* (ARIZ).

- 2b. ***Hesperaloe funifera*** (Koch) Trel. subsp. ***chiangii*** G. D. Starr subsp. nov. (Fig. 3)—TYPE: MEXICO, San Luis Potosí; km 144 on Mexico highway 57 between Matehuala and San Luis Potosí to the west of the pueblito of Pozos Santa Clara, in grasslands with *Agave scabra*, *Cassia wislizenii*, *Koeberlinia spinosa*, *Larrea divaricata*, *Prosopis laevigata*, and *Yucca australis*, 23°15'N, 100°33'W, 1500 m, *E. Garcia Moya s.n.* (holotype: DES!).

Subspecies haec ab *H. funifera* ssp. *funifera* differt planta rhizomatosus longissimus, foliis 6 cm latis, marginalis fibris incrassatus ad 2–3 mm.

Plants acaulescent, long rhizomatous, forming wide clumps or fairy rings to 2 m or more in diameter. Leaves stiff, erect, medium to dark green, deeply canaliculate, lanceolate, reaching 1.5 m long, 5–6 cm wide (when flattened) from the base to the middle, tapering from the middle to the apex, the marginal fibers coarse, 2–3 mm diameter, white to gray near point of attachment, straight to slightly coiled.

Phenology and distribution (Fig. 1). Flowering period for ssp. *chiangii* is currently unknown. When three populations were visited in August 1990 only the population near Santo Domingo, San Luis Potosí, showed evidence of flowering that year. Flower stalks with ripe capsules were present and seed was collected. *Hesperaloe funifera* ssp. *chiangii* is geographically separated from ssp. *funifera*. The subspecies *chiangii* is locally common on flats and open slopes



FIG. 3. *Hesperaloe funifera* ssp. *chiangii*. A. Habit. B. Leaf lower 1/5th. C. Leaf upper 1/5th. D. Inflorescence. E. Inflorescence showing bract. F. Flower. G. Flower cross section. H. Portion of infructescence with capsule. I. Seed.

in San Luis Potosí. Average annual precipitation ranges from 300–600 mm. Associated plants include *Acacia* spp., *Agave* spp., *Fouquieria splendens*, *Prosopis laevigata*, and *Yucca filifera*.

Paratypes. MEXICO. San Luis Potosí: Hacienda de Angostura, 5 Aug 1891, *Pringle 3911* (UC, MO, NY, F, MICH); 12 miles NW of Cd. del Mais along highway to Cd. San Luis Potosí, 19 February 1951, *E. C. Ogden, C. L. Gilly, and E. Hernandez. 51119* (ARIZ); km 570 carretera Mexico-Piedras Negras, 18 May 1957, *Rzedowski*

8709 (TEX); near Santo Domingo, Hwy 80, 26–28 January 1952, *H. S. Gentry 11512* (ARIZ).

3. *Hesperaloe nocturna* H. S. Gentry, *Madroño* 19:74–78. 1967.—
TYPE: MEXICO, Sonora; 15 miles SE of Magdalena along road to Cucurpe, by Sierra Baviso, 3,200–3,500 feet, 21 May 1963, *Gentry and Felger 19988* (holotype: US!).

Plants densely caespitose, forming clumps to 1–2 m across. Leaves upright and arching, linear, 1–1.5 m long, 1–2 cm wide at base, long attenuate at apex; margins narrow, brown, finely filiferous with white, irregularly wavy fibers. Inflorescence a slender panicle to 1.5–4 m high, with 2–3 branches in upper one-half. Flowers nocturnal, campanulate-rotate, in indeterminate fascicles; tepals greenish-white on adaxial face 15–25 mm long, abaxial face of inner tepals with broad, reddish-purple center stripe, 8–9 mm wide, abaxial face of outer tepals reddish with greenish-brown center stripe, 6–7 mm wide; stamens and pistil included; filaments attached to base of tepals for 3 mm; ovary at anthesis 10 mm long and 4 mm wide; pedicels 14–16 mm long. Capsules depressed ovoid or oblong, 3–4 cm long, 2.5–4.5 cm wide, short beaked; seeds black, 11 mm long, 8 mm wide.

Phenology and distribution (Fig. 1). Flowering occurs from Apr to Jul, with seed set coinciding with summer rains. Known only from north-central Sonora at 950–1150 m elevation with *Acacia occidentalis*, *Acacia greggii*, *Berberis haematocarpa*, *Cercidium floridum*, *Coursetia microphylla*, *Fouquieria splendens*, *Prosopis velutina*, and *Yucca arizonica*. Also reported from one sterile specimen in northeastern Sonora where it was growing on a steep canyon wall with *Ficus petiolaris*, *Justicia candicans*, and *Quercus* sp.

Specimens examined. MEXICO. Sonora. 20.4 miles SE of Magdalena on Cucurpe road, 11 Apr 1976, *T. R. Van Devender*, *K. B. Moodie*, and *S. F. Hale* (ARIZ); Rancho Noria Aguilarena, N of Ures and Santiago, 29°33'N, 110°25'–26'W, 500 m, 9 Jul 1992, *E. Joyal 2054* (ARIZ); Cañon de la Bota, N end of Sierra el Tigre, 34 km (air) ESE of Esqueda, near 30°36'N, 109°13'W, 3300–3600 ft., 31 Jan 1982, sterile specimen, *G. Yatskievych 82-54* (ARIZ); 15 miles SE of Magdalena to Cucurpe, 3200–3300 ft, 21 May 1963, *R. S. Felger 7942* and *H. S. Gentry* (ARIZ); 17 miles SE of Magdalena, Palm Canyon in Cerro Cinta de Plata, 5 Jun 1978, *T. R. Van Devender s.n.* (ARIZ); 15 miles SE of Magdalena, 3000–3400 ft, 21 May 1963, *R. S. Felger and H. S. Gentry 19988* (ARIZ); 17 miles SE of Magdalena, 11 Sept 1934, *I. L. Wiggins 7132* (ARIZ).

4. *Hesperaloe parviflora* (Torrey) J. M. Coulter, *Contributions from U.S. National Herbarium*. 2:436. 1894.—*Yucca parviflora* Tor-

rey, Botany of the Boundary of Emory's Report of the U.S. and Mexican Boundary Survey, 221. 1859.—*Aloe yuccaefolia* A. Gray, Proceedings of the American Academy of Arts and Sciences, 7:390. 1867., illegit., based on *Hesperaloe parviflora* (Torrey) J. M. Coulter.—*Hesperaloe yuccaefolia* (A. Gray) Engelm., in C. King, Geological Exploration of the 40th Parallel, 5, 497. 1871., illegit., see preceding.—SYNTYPES: USA, Texas; "Gravelly hills near the mouth of the Pecos", Bigelow s.n. Stony hills west of the Nueces river, Wright 1908. (lectotype: GH!; isolectotype: NY!)

Hesperaloe engelmanni Krauskopf, Notice to Botanists. (circular). 1878.—TYPE: none designated. *Hesperaloe parviflora* (Torrey) Coulter [var.] *engelmanni* (Krauskopf) Trelease, Annual Report of the Missouri Botanical Garden, 13:33. 1902.—TYPE: none cited; placed in synonymy here; see discussion under taxonomy.

Plants densely caespitose, forming clumps to 1 m or more wide. Leaves dark green, arching, 30–60 (120) cm long, 8–18 mm wide at base, narrowing to apex, linear, margin finely filiferous, with tightly curled fibers. Inflorescence branched panicle to 1–2.5 m long, the few branches mainly in upper one-half. Flowers diurnal, tubular or oblong-campanulate, in indeterminate fascicles; tepals salmon, coral, pink, or rosy-red, one horticultural selection is yellow, the outer 15–20 mm long, 4–7 mm wide, the inner 17–20 mm long, 5–8 mm wide; stamens included, the filaments 7–13 mm long, attached to base of tepals for 1 mm, anthers 2–3 mm long; ovary 4–6 mm long, 3–4 mm wide at anthesis, style included. Capsule ovoid or oblong-ovoid, 30–40 mm long, 25–30 mm wide, beaked, long pedunculate, rugose; seeds black 9–10 mm long, 6–7 mm wide. *Hesperaloe parviflora* occurs in *Larrea* desert, oak and chaparral zones from 600–2000 m in northwestern Coahuila, and Val Verde, Mills, San Saba, Haskell and Collin Counties in Texas.

Phenology and distribution (Fig. 1). Flowering period for *Hesperaloe parviflora* ranges from March through September. The species is known from central Texas in the Edwards Plateau region and adjacent Mexico.

Taxonomy. In 1859, Torrey described *Yucca parviflora* from gravelly hills near the mouth of the Pecos (Bigelow s.n.) and stony hills west of the Nueces, Texas (Wright 1908). Then in 1867, Gray decided that the taxon fit into *Aloe* better than *Yucca* and described *Aloe yuccaefolia*. Gray used Wright 685 with flowers and mature fruit and Wright 1908, the same collection used by Torrey for his description of *Yucca parviflora*. Gray (1867) used the specific epithet of *yuccaefolia* because there was already an *Aloe parviflora*. In 1871, Engelm. created the genus *Hesperaloe* and transferred the

recently described *Aloe yuccaefolia*. However, *Yucca parviflora* has priority making the correct combination *Hesperaloe parviflora* (Torrey) Coulter. Krauskopf (1878) proposed the name *Hesperaloe engelmanni* for plants with longer anthers and a short, thick (not filiform) style. These plants were collected along the western branch of the Nueces river while the plants Wright collected came from near the Nueces river and Devil's river. These localities are close enough that neither specific nor subspecific rank should be maintained for those plants until more field research can be done.

Specimens examined. USA. Texas: Mills Co., 1 mile W of Center City on route 84, 27 May 1964, C. E. Smith Jr. and H.-S. Gentry 4322 (ARIZ); MEXICO. Coahuila: ca. 12 air miles E. of Boquillas, 83 road miles NW of Rancho El Jardin, 29°10'N, 102°44'W, 27 July 1973, J. Henrickson 11488 (ARIZ); Los Cojos Minas, SW slope of Sierra del Carmen, 11 October 1972, R.G. Engard and H.S. Gentry 23118 (ARIZ).

5. ***Hesperaloe tenuifolia*** G. D. Starr sp. nov. (Fig. 4)—TYPE: MEXICO, Sonora; 24 km (airline) northeast of Alamos, near Rancho Santa Barbara on Cerro Agujudo, 108°43'43"W, 27°06'50"N, elevation 1500 m, 16 May 1990, S. Meyer and P. Jenkins 9063 (holotype: ARIZ!)

Planta acaulis, cespitosa, 0.5 m lata; foliis linearis-longiapiiculatis, 0.5–1 m longis, 0.5–1 cm latis ad basim, margine angusto sparse filifero; inflorescentia paniculata, 1.5–2 metralis; flores pedicillati, tepala exteriora dorsaliter rosea mediane brunneo-virido ventraliter albida margine rubro, interiora dorsaliter obscure rosea margine albo ventraliter albida, 15 mm longa, 3 mm lata; antheris inclusis, capsulae ovoideae, 2–3 cm longae, 2–2.5 cm latae; semina nigra 6–9 mm longa, 5–6 mm lata.

Plants acaulescent, sparsely caespitose, forming small clumps to 0.5 m wide. Leaves arching, narrowly linear 0.5–1 m long, 0.5–1 cm wide at the base tapering to the apex, margins thin, finely filiferous, fibers white and not tightly curled. Inflorescence raceme or 2–3 branched panicle, to 1.5–2 m long. Flowers nocturnal, rotate; outer tepals linear, 13 mm long, 5 mm wide, dorsal side dark pinkish-red, ventral face white with reddish margin; inner tepals ovate, 15 mm long, 8 mm wide, dorsal side dark pinkish-red with white margin, ventral face white; anthers included, attached to base of tepals for 2 mm, filaments 9 mm long, anther sacs 3 mm long; ovary 6 mm long, 3 mm wide, style 4 mm long. Capsule ovoid, 2–3 cm long, 2–2.5 cm wide, beak none or to 1 mm long; seeds black, 10 mm long, 5–7 mm wide.

Phenology and distribution (Fig. 1). Flowering occurs primarily in April and May with seed maturing in June and July. *Hesperaloe*

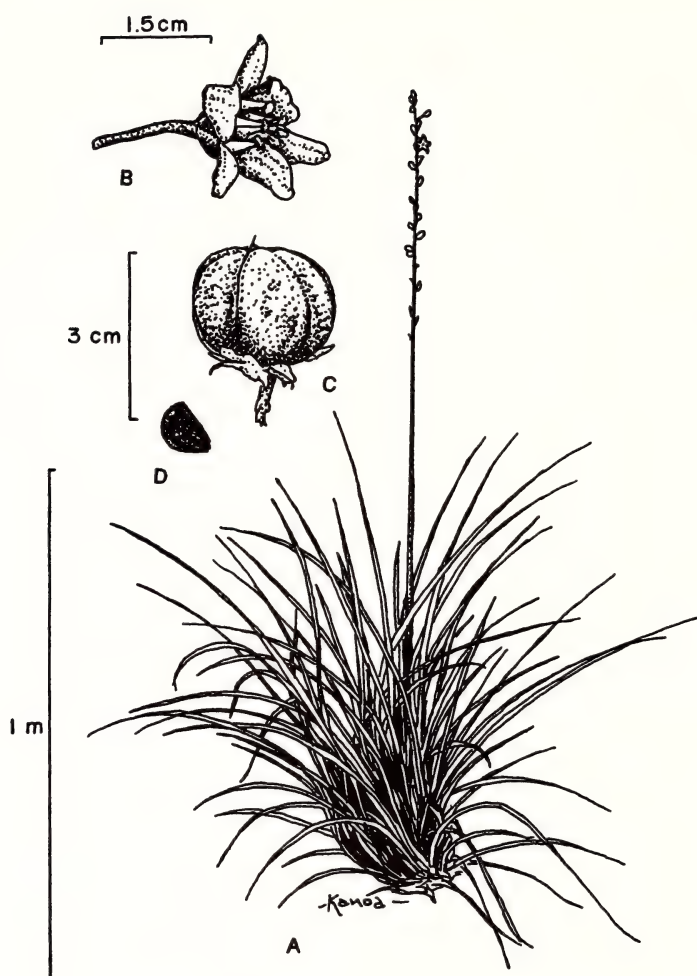


FIG. 4. *Hesperaloe tenuifolia* A. Habit. B. Flower. C. Capsule. D. Seed.

tenuifolia is known only from the Cerro Agujudo northeast of Alamos, Sonora. Plants grow on rhyolitic rock on dry hilltops at 1500 m with *Pinus oocarpa*, *Pinus leiophylla*, and *Quercus tarahumara*.

HORTICULTURE

Hesperaloe has been cultivated in the United States since at least 1878 when Krauskopf offered for sale plants that he collected along the western branch of the Nueces River in western Texas. Prior to that, plants were grown at the botanical gardens in Cambridge from

material Wright collected in 1849. All species are best used in full or reflected sun, and a fast draining soil. The growth rate varies from fast (flowering in 4 years from seed) to moderately fast (flowering in 5 years from seed). The fast growing species are *H. parviflora* and *H. tenuifolia*, and the slower growing species are *H. campanulata*, *H. nocturna*, and *H. funifera*. *Hesperaloe* has CAM metabolism so growth occurs year round. Because of this, they can be grown faster by applying fertilizer and consistent, thorough waterings all year. Amount of fertilizer and water applied will vary with temperature though. All species are quite drought tolerant once established. They will survive on less than 12" of annual precipitation and can go for 2 months or more without supplemental water. No maintenance is required except for removal of old flower spikes if so desired. All species are hardy to at least 15° F with *H. funifera* and *H. parviflora* being hardy to at least 10° F. The flowering period for all species is usually longer for cultivated plants than for wild populations. The application of supplemental water and the warmer temperatures of cities versus the open desert results in flower spikes appearing earlier and persisting later in the year. The flowers of *H. parviflora* are visited by hummingbirds as well as bees. Flowers of *H. funifera*, *H. nocturna*, and *H. tenuifolia* are visited by bats and hawk moths. *Hesperaloe campanulata* flowers are visited by bats and hawk moths at night, and visited by hummingbirds and bees by day.

HYBRIDS

Hybrids in *Hesperaloe* are known to occur. Hybrid plants that were results of the crosses *H. nocturna* × *H. parviflora* (pollen parent undetermined) and *H. parviflora* (male) × *H. funifera* (female) have been observed. F₂ offspring from the *H. parviflora* × *H. funifera* hybrid plants have also been observed. These plants were still young, however some were of flowering age and did show segregation of flower characteristics back towards the parent species. The progeny of *H. nocturna* × *H. parviflora* had the flower color of *H. parviflora* and flower shape intermediate, while the leaves were more like *H. nocturna*. I have made crosses between *H. campanulata* (male) × *H. funifera* (female) and *H. campanulata* (male) × (*H. parviflora* × *H. funifera*) (female). I made the *H. campanulata* × *H. funifera* cross after visiting the unusual *H. funifera* population in western Nuevo Leon. The proximity to both *H. campanulata* and *H. funifera*, along with the variation in flower color within this population, gave me the impression that the plants were of hybrid origin. It is also possible that these plants are the result of a *H. parviflora* × *H. funifera* cross. However, all the flowers had tepals that were flared open like *H. funifera*, whereas I would expect to see flowers

similar to both parents in a segregating population. It seems unlikely that these could be F_1 plants because there are no known populations of *H. parviflora* in the vicinity. Seed has been collected and plants are being grown to further study this variant of *Hesperaloe*. *Hesperaloe campanulata* also is of possible hybrid origin. *Hesperaloe funifera* and *H. parviflora* may have crossed at some point in the past and *H. campanulata* and the unusual plants in western Nuevo Leon could be descendants of that cross. In the field, flower color and shape of *H. campanulata* were consistent, while leaf size was variable. This leads me to conclude that *H. campanulata* is a stable species. However, the population of *H. funifera* in western Nuevo Leon appears to be simply a color variation and therefore not recognizable as a distinct taxon.

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NOTES

THE MONOTROPOIDEAE IS A MONOPHYLETIC SISTER GROUP TO THE ARBUTOIDEAE (ERICACEAE): A MOLECULAR TEST OF COPELAND'S HYPOTHESIS. Kenneth W. Cullings, Department of Biology, San Francisco State University, San Francisco, CA 94132 and Lena Hileman, Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA 02138.

The Monotropoideae (Ericaceae) is a group of plants, mostly California natives, with an achlorophyllous, mycotrophic habit; all plants in this subfamily depend upon shared mycorrhizal connections with neighboring photosynthetic plants for carbon nutrition (Björkman, *Physiologia Plantarum* 13:309–327, 1960). These associations can be quite specific; the most specific mycorrhizal association of any kind is between *Pterospora andromedea* and the mycorrhizal fungus *Rhizopogon* (Cullings et al., *Nature* 379:63–65). The morphology and physiology of these symbioses can be defining characters in the taxonomy of the Monotropoideae and related subfamilies of the Ericaceae (Cullings, *Journal of Evolutionary Biology* 7:501–516, 1994; Cullings et al., *Nature* 379:63–65, 1996), and detailed molecular analysis of relationships among members of the Monotropoideae with respect to these characters has been described (Cullings, *Journal of Evolutionary Biology* 7:501–516, 1994).

Both morphological (Copeland, *Madroño* 6:97–119, 1941; Wallace, *Bot. Notiser* 128:286–298, 1976) and molecular evidence (Cullings and Bruns, *Canadian Journal of Botany* 70:1703–1708, 1992; Cullings, *Journal of Evolutionary Biology* 7:501–516, 1994) strongly indicate that the bulk of the Monotropoideae share a most recent common ancestor with the Arbutoideae (Ericaceae). However, morphological heterogeneity prompted Copeland (*Madroño* 6:97–119, 1941) to hypothesize that the Monotropoideae may be polyphyletic within the Arbutoideae. Recently, Cullings (*Journal of Evolutionary Biology* 7:501–516, 1994) provided strong molecular evidence that one monotropoid species, *Monotropis ordata*, is in fact most closely related to members of the Vaccinioideae, and that the Monotropoideae is polyphyletic. Furthermore, this study confirmed the close association between the bulk of the Monotropoideae and Arbutoideae. However, as the sampling of members of the Arbutoideae was limited to two *Arctostaphylos* species, Copeland's hypothesis that the Monotropoideae has more than one origin within the Arbutoideae has not been fully addressed using molecular methods.

In this study, partial 28S nuclear ribosomal RNA (nrRNA) gene sequences were used to test Copeland's hypothesis. Sequences were generated using the polymerase chain reaction (PCR) and plant-specific primers developed by Cullings (*Molecular Ecology* 1(4):233–240, 1992). PCR products were sequenced directly using the asymmetric primer ratio method (Gyllenstein and Erlich, *Proceedings of the National Academy of Sciences U.S.A.* 85:7652–7658, 1988) and resulted in 500 bases of easily alignable sequence with 2 small indels that were omitted from the analysis. Data were analyzed cladistically using PAUP vers. 3.1.1 (Swofford, D. L. Computer program distributed by Illinois Natural History Survey, Champaign, Ill, 1995), and by neighbor-joining using PHYLIP vers. 3.572. All analyses were performed with characters unweighted, and bootstrapping was used to assess strength of clades. Trees were rooted by the outgroup comparison with *Clethra* (Clethraceae, Ericales).

Results of this study indicate that the Monotropoideae and Arbutoideae are monophyletic sister groups (Fig. 1), and thus do not support Copeland's hypothesis that the bulk of the Monotropoideae are polyphyletic within the Arbutoideae. Relationships within the Monotropoideae depicted by parsimony analysis of 28S rRNA data have been reviewed previously, and are supported by both morphological and bio-

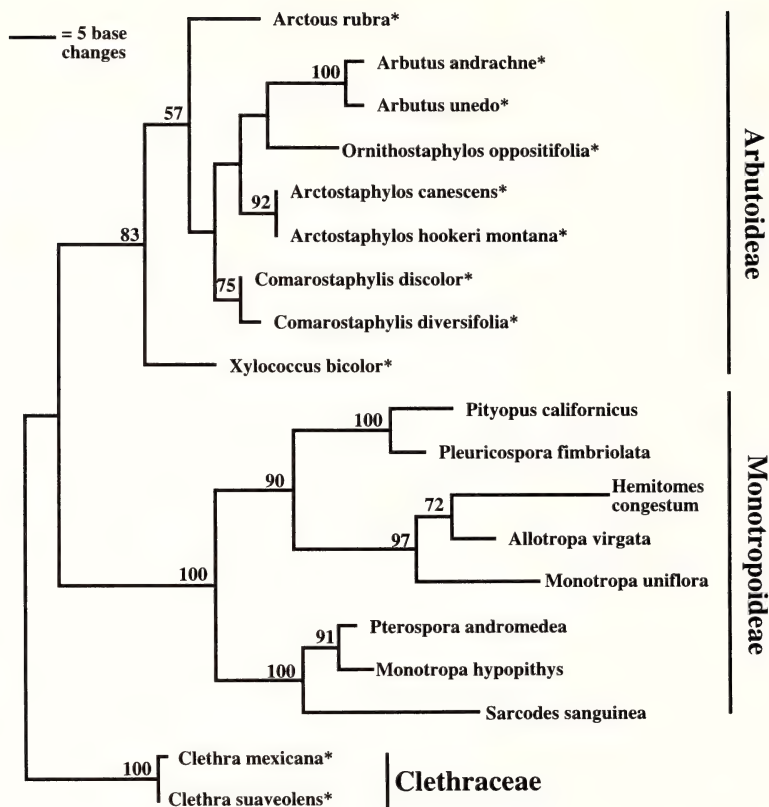


FIG. 1. Phylogeny of the Arbutioideae and Monotropoideae based on partial 28S ribosomal RNA gene sequences. Analysis resulted in a single most parsimonious tree with length: 234, C.I.: 0.709, R.I.: 0.796, rescaled C.I.: 0.565. Numbers at nodes are bootstrap indices of support (1000 replicates). New sequences are indicated by *, all others have been published previously (Cullings, Journal of Evolutionary Biology 7: 501–516, 1994). Tree is drawn to scale shown.

chemical data (Cullings, Journal of Evolutionary Biology 7:501–516, 1994). Relationships within the Arbutioideae are unresolved by these data (Fig. 1); genera are well supported as monophyletic, but relationships among genera could not be resolved. These relationships are currently being determined using the internal transcribed spacer (ITS), a more rapidly evolving portion of the rRNA repeat unit (Jorgenson and Cluster, Annals of the Missouri Botanical Garden 75:1238–1247, 1988).

Taken together, molecular data provide a comprehensive picture of evolutionary patterns within a broadly defined Ericaceae. Both nuclear (28S rRNA) and chloroplast (rbc-L) data indicate that the Arbutioideae split from the Ericaceae relatively early, and that the ericoid mycorrhiza-formers, a group that includes the bulk of the Ericaceae, plus the Empetraceae and Epacridaceae (Kron and Chase, Annals of the Missouri Botanical Garden 80(3):735–741, 1993; Cullings, Canadian Journal of Botany in press), form a derived group relative to the Arbutioideae. Nuclear data provide further resolution, and indicate that the Ericaceae split into two main groups, the

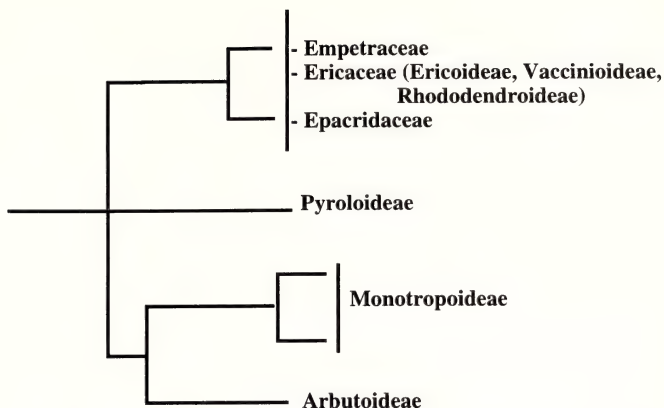


FIG. 2. Schematic of evolutionary trends within the Ericaceae based on a consensus of chloroplast (*rbc-L*) and nuclear (28S rRNA) DNA data. Tree indicates that the arbutoid and monotropoid mycorrhiza-forming groups, Arbutoideae and Monotropoideae, form a monophyletic sister group to the ericoid and pyroloid mycorrhiza-formers, and that the position of the Pyroloideae is unresolved by molecular data.

arbutoid/monotropoid mycorrhizae formers, a clade consisting of the Arbutoideae and Monotropoideae, and the ericoid mycorrhiza-formers (Cullings, *Journal of Evolutionary Biology* 7:501–516, 1994) (Fig. 2). The Pyroloideae, a group that forms mycorrhizae that are intermediate in form, cannot be placed within either clade. Based on this, it appears that one of the pressures influencing cladogenesis within the Ericaceae may have been nutrient access via different mycorrhizal strategies, with the ericoid mycorrhiza clade liberating nutrients from acidic soils (Cullings, *Journal of Evolutionary Biology* 7:501–516, 1994; Specht, *Heathlands and Related Shrublands*, R. L. Specht (ed.), Elsevier Scientific Publishing Company, New York, 1977), and the arbutoid/monotropoid clade receiving carbon through mycorrhizal connections with ectomycorrhizal fungi shared in common with neighboring trees. Members of the Monotropoideae have taken this strategy to the extreme, and have become achlorophyllous and wholly dependent upon these shared mycorrhizal connections (Björkman, *Physiologia Plantarum* 13:309–327, 1960; Cullings et al., *Nature* 379:63–65, 1996). However, because the Monotropoideae are achlorophyllous, it is likely that much of their chloroplast genome has been reduced or lost, as in the case of the achlorophyllous plant parasites in the Orobanchaceae (dePamphilis et al., *Nature* 348: 337–339, 1991). Thus, corroborating data from chloroplast DNA may not be possible with *rbc-L*, though other chloroplast loci may prove useful. At present this possibility is being explored.

LECTOTYPIFICATION OF *SETARIA TENAX* VAR. *ANTRORSA* (GRAMINEAE).—Laurence J. Toolin, Herbarium, Shantz 113, University of Arizona, Tucson, AZ 85721.

Setaria tenax (Rich.) Desv. (*Panicum tenax* Rich.) is a neotropical perennial in the subgenus *Setaria* that ranges from southern Mexico to northern South America. The type (FI; fragment, US!) was collected in Cayenne, French Guiana. Within its range, *S. tenax* is best distinguished from its congeners by the following combination of characters: the awns subtending the spikelets bear both antrorse and retrorse barbs; the spikelets are 2.2–2.5 mm long and somewhat hemispheric; the first glume is one-

third as long as the spikelet, and the second glume is about one-half the spikelet length; the fertile lemma is strongly gibbous, transversely rugose below, becoming smooth and shiny at the apex.

In 1962 (Illinois Biol. Monogr. 29, p. 44.), J. M. Rominger described a variety, *antrorsa*, of *Setaria tenax*. He indicated the type locality as Chichén Itzá, Yucatán, Mexico, citing *Swallen 2439*, with specimens deposited at both MO and US, but did not designate either of the specimens as the holotype. He noted that his new variety differed from var. *tenax* solely in having only antrorse barbs on the awns, with no retrorse barbs present. Var. *antrorsa* is known from the Mexican states of Yucatán, Veracruz, and Chiapas, as well as Honduras (R. W. Pohl, *Flora Mesoamericana* 6: 360, 1994).

The US specimen of *Swallen 2439* was examined as part of a study comparing some North and South America taxa to verify the occurrence of certain species in both hemispheres. It was noticed immediately that Rominger had never annotated the sheet, and this had been noted on the specimen by D. H. Nicholson. The US folder is labeled "possible isotype". The MO specimen also has no annotation by Rominger. The MO sheet was annotated as an isotype by G. Davidse, who may have simply assumed that the holotype was at US. Pohl (*l.c.*), who seems to be the only author to deal with var. *antrorsa* since Rominger, states the following: "Holotipo: Mexico, Yucatán, *Swallen 2439* (US!)." Pohl is obviously incorrect here, since Rominger himself did not select the US specimen as holotype, and, moreover, listed MO ahead of US in citing the type specimens. How Pohl came to consider the US specimen to be the holotype is a mystery. Rominger, in a recent conversation, told me that he had never had any discussion with Pohl regarding var. *antrorsa*, and encouraged my selecting a lectotype. Pohl's published citation, left uncorrected, constitutes a potential source of confusion.

Article 9.9 of the Tokyo Code (1994) provides for the lectotypification of a taxon where a holotype is not designated in the original protologue. Lectotypification of *Setaria tenax* var. *antrorsa* is therefore proposed here.

The MO and US specimens of var. *antrorsa* are not of equal quality. The US sheet has a single culm with an immature panicle. The young spikelets are not mature enough to exhibit adequately the *Setaria tenax* characters given above. The MO specimen, in contrast, has two mature panicles in which the spikelets are well-developed and typical of the species. Because the latter specimen clearly better represents the species, and because Rominger cited the MO specimen first in his protologue, I designate *Swallen 2439* at MO (sheet No. 1043993) as the lectotype of *Setaria tenax* var. *antrorsa*; the US specimen (sheet No. 3090500) then becomes the isolectotype.

REPRODUCTIVE RESPONSE TO FIRE BY THE LAUREL SUMAC, *MALOSMA LAURINA* (ANACARDIACEAE).—Gary B. Perlmutter, 151 N. Lomita Avenue, Ojai, CA 93023.

One of the adaptations perennial plants have to an environment with frequent fires or other stresses is the ability to sprout from surviving structures within the soil after the aerial portions have been destroyed by the disturbance. These subterranean features include rhizomes, bulbs, and undamaged root crowns. Many such fire resistant species produce flowers either immediately following or more than two years after the plant is burned (Gill, Fire and the Australian Biota, Australian Academy of Science, Canberra, 1981; Platt et al., *Oecologia* 76:353–363, 1988).

Malosma laurina (Nutt.) Abrams (laurel sumac) is a facultative resprouter (Saruwatari and Davis, *Oecologia* 80:303–308, 1989) with year-round growth in coastal environments of southern California (Watkins and de Forest, *Ecology* 22:79–83, 1941). While its growth patterns and seedling survivorship following fire disturbance have been studied (Thomas and Davis, *Oecologia* 80:309–320, 1989), the repro-

ductive effects of this species have been overlooked. Is flowering hindered by vegetative growth in burn recovery or do plants flower the following summer regardless of canopy damage by a recent fire? The data presented here aim to answer this question.

Phenological patterns of inflorescences of burned and unburned sumacs were studied in habitats of similar climate along coastal slopes of the Santa Monica Mountains (34°05'N, 119°02'W) in southeastern Ventura County. The climate is of the South Coast Thermal Belt with mild winters and summer heat modified by marine influence (Hickman, The Jepson manual: higher plants of California, University of California Press, 1993). One of these sites was burned by the Green Meadow Fire in October 1993 while two others were spared by the fire. Reconnaissance of the area for site selection in November 1994 revealed sprouting shrubs about 1 m tall scattered throughout a successional grassland except for a few patches of unburned coastal sage scrub where large *M. laurina* shrubs flourished. Site descriptions are as follows:

The burned site lies at the Mugu Peak trailhead at the base of a southwest-facing slope at 6 m elevation. The plant community was a successional grassland dominated by *Nassella* sp., *M. laurina*, and *Malacothamnus fasciculatum*. The soil was a pebbly loam with a water capacity of 0.43 cm/cm. *Malosma* shrubs were stump-sprouting, with conspicuous burnt branches extending beyond the living canopies. Down the coast, 4 km ESE from this site is the site Unburnt 1. Also at 6 m elevation, it lies at the base of a south-facing slope just east of La Jolla Canyon. The community is Diegan Coastal Sage Scrub (Holland, Preliminary descriptions of the terrestrial natural communities of California, California Department of Fish and Game, 1986) dominated by *Artemisia californica*, *M. laurina*, and *Salvia mellifera*. *Malosma* canopies were interwoven to form a nearly continuous horizontal band at that altitude for 1 km. The soil is a fine sandy/silty loam with blocky talus and 0.13 cm/cm water capacity. The site Unburnt 2 lies 8 km ESE of the burned site, along Deer Creek Rd at 150 m elevation on a northeast-facing slope. This was in a low, 1 m high chaparral dominated by *Lotus scoparius*, *Ceanothus megacarpus*, and *M. laurina*. Although the community structure and composition suggests second-year fire succession (McAuley, Wildflowers of the Santa Monica Mountains, Canyon Publishing Co., 1985), study shrubs showed no fire damage. The soil was a gravelly loam with 0.46 cm/cm water capacity.

At each site, five representative individuals at least 2 m tall were selected for study and marked with flagging. Beginning in May 1995, sites were visited weekly to record the presence and condition of inflorescences at each plant. Panicle condition was classified and ranked into the following stages: growing buds (1), mature buds (2), and flowers (3). The growing bud stage is characterized by a reddish color and small size; the mature bud stage exhibits greenish, pinkish or whitish color and larger size. Each plant canopy was divided into four sections (north, east, south, and west faces) to bring the sample size to 20 per site; in each section I recorded the stages panicles were observed in.

From the data, onset and peak dates of each stage were determined and compared among sites, as were flower development periods (D_{F1}), which is here defined as the number of weeks from the date of first buds observed to the date when at least 50% of a population is in flower (Bowers, Madroño 43(1):69–84). Stage onset dates of each shrub were further compared to assess within-site variation.

Burned shrubs showed no panicles from previous seasons, whereas inflorescences were abundant on unburned plants. Onset and peak dates of bud and flower stages were up to 5 wk later among burned shrubs (Fig. 1); however, D_{F1} was 8 wk in each site.

Within sites, onset dates of individual shrubs varied 1–4 wk (Fig. 2). In the burned site, this variance for the growing bud, mature bud and flower stages are 4, 3, and 1 wk, respectively; in Unburnt 1 these are 1, 4, and 4 wk; and in Unburnt 2 they are 2, 4, and 3 wk.

In the burned site, *Malosma laurina* resprouters did not produce flowers until two

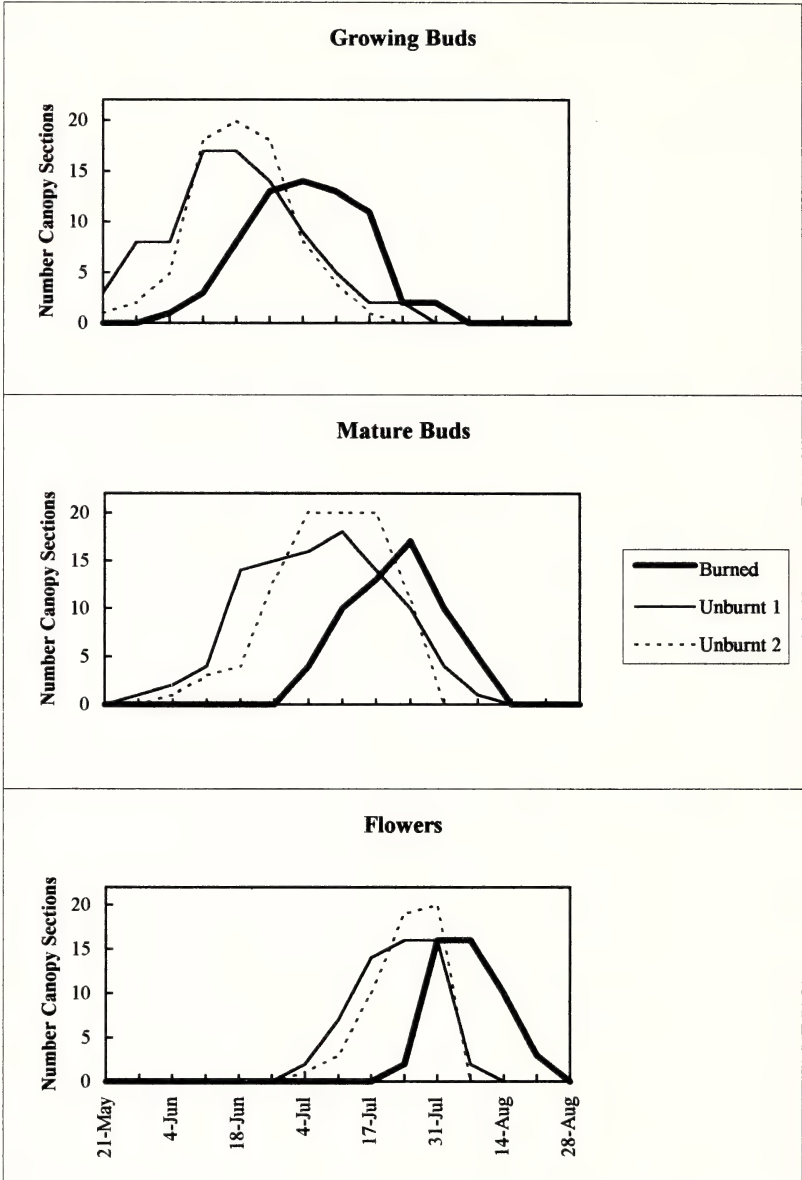


FIG. 1. Phenograms of burned and unburned study populations of *Malosma* in the Santa Monica Mountains, 1995 ($n_i = 20$).

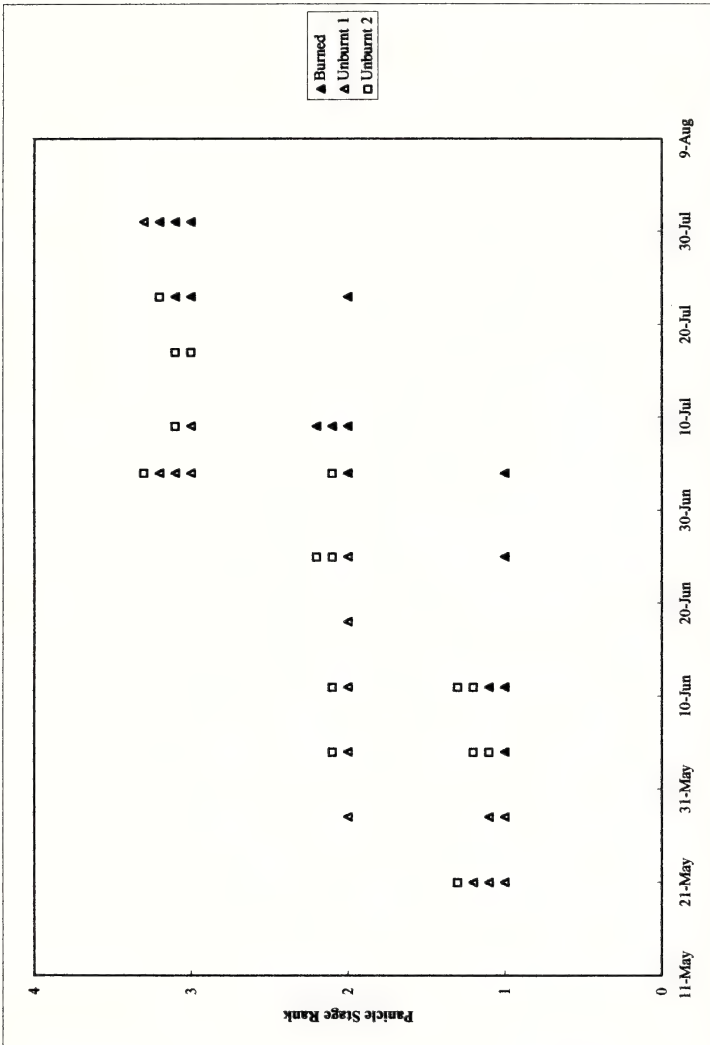


FIG. 2. Onset dates of bud and flower stages by rank of individual *Malosma* study plants in burned and unburned sites in the Santa Monica Mountains, 1995.

years after the fire, when plants approached 2 m height. Many fire resistant shrubs in Australia have a similar response (Gill, 1981). Flowering in this species seems to be related to plant vigor, which could be indicated by shrub size or time of recovery. As for size, Florida scrub plants had to attain a minimum stem diameter before producing flowers after a fire (Ostertag and Menges, *Journal of Vegetation* 5:303–310, 1994). This seems unlikely for *Malosma*, since the sizes of burned shrubs varied (1.5–2.5 m height by 1.5–4.0 m width, estimated). Canopy sizes were observed to be in direct proportion to their extended burned branches (no data collected), which is likely proportional to the sizes of their root crowns. Furthermore, the delay period of two years by resprouters did not vary, which suggests that a certain amount of time is required for these shrubs to recover in order to make a reproductive effort.

This second year response among burned shrubs, plus the observed delay in the development of inflorescences as compared to the unburned populations, could be explained by the investment of energy toward vegetative growth in fire recovery. Throughout the season this growth was observed in all study plants, and more pronounced among resprouters (no data collected). Two earlier studies of *M. laurina* populations in the Santa Monica Mountains illustrate a drastic increase in vegetative growth by resprouting shrubs. During the primary growing season from February through July, Thomas and Davis (1989) reported shoot elongation of 16 cm per month by resprouters in the first year after a fire. This is about ten times the growth rate of that reported for undisturbed shrubs (1.8 cm per month) during the same period by Watkins and de Forest (1941).

Alternatively, the delay in panicle emergence and development could be explained by population genetics. Each study population is separated by a distance of 4 km, which make it unlikely for these populations to interbreed, due to the foraging patterns of their insect vectors. However, *Malosma* shrubs were found throughout the areas between sites, thus being part of a larger contiguous population. The reconnaissance visit in 1994 revealed morphological similarity among resprouters (i.e., no panicles observed at one year after fire) at Pt. Mugu, La Jolla Canyon, Sycamore Canyon, and along Deer Creek Rd. Therefore, it seems unlikely that the burned population exhibited phenological patterns that were unique to that population. A genetic analysis of selected plants in these locations could reveal how similar the above populations are.

As the within-site variation of bud and flower onset indicate, the observed within-season delay of the burned population is not significant. The greater number of onset dates shared by shrubs in the burned site and Unburnt 2, which have similar soil water capacities, than the former and Unburnt 1, where these are different, suggests that soil moisture also influences timing and development of flowers, but to a lesser degree than fire disturbance.

I am grateful to Dieter H. Wilken of the Santa Barbara Botanic Garden for his advice throughout the study. I also wish to thank Ray Sauvajot of the National Park Service, David A. Young, and an anonymous reviewer for their helpful comments to earlier drafts of the manuscript, while Steven G. Lawry of Lawry's Technical Services provided transportation to and from sites. Fieldwork was conducted under a Research Permit issued by the Santa Monica Mountains National Recreation Area with verbal permission from Point Mugu State Park.

NOTEWORTHY COLLECTIONS

CALIFORNIA

DODECAHEMA LEPTOCERAS (A. Gray) Rev. & Hardham (POLYGONACEAE).—Riverside Co., between 13 and 16.2 km E of Temecula, S of Vail Lake, in and adjacent to the Arroyo Seco and Kolb Creek drainages, 455 to 550 m, in Temecula Arkose formation, 5 May 1989, *Gordon-Reedy s.n.* (SD). Bare or sparsely vegetated benches above drainages, openings in chaparral, or understory (leaf litter) of oak trees. Associated species: *Adenostoma fasciculatum*, *Adenostoma sparsifolium*, *Eriogonum fasciculatum* ssp. *foliolosum*, *Eriastrum sapharinum*, *Stylocline gnaphalioides*, *Vulpia myuros* var. *hirsuta*, *Chorizanthe coriacea*, *Salvia columbariae*, *Nemacladus longiflorus*, *Lupinus bicolor*, and *Chaenactis glabriuscula*.

Previous knowledge. *Dodecahema leptoceras* had an historical distribution along the southern margin of the San Gabriel, San Bernardino, and San Jacinto mountains, where it was documented on sandy, flood-deposited river terraces and washes below about 670 m, in association with intermediate to older successional phases of alluvial scrub habitat. Although this species had been recorded from over 20 localities, only 5 extant sites were known prior to this occurrence, and most of these were relatively small (<2000 individuals) and/or unprotected.

Significance. The Vail Lake population represents (1) a new location for this federally and state-endangered species, (2) a southward range extension of approximately 25–27 km from the nearest known locality along Bautista Creek, (3) the largest known population, and (4) an occurrence in “atypical” habitat. Population size was estimated at approximately 10,000 individuals in 1989. Re-surveys of the area in 1990 revealed population increases at most locations, for a revised population estimate of 19,000 individuals. A portion of the population occurs on U.S. Forest Service land, thereby receiving some degree of protection. While part of the population occurs in typical floodplain habitat (i.e., benches above the main drainage), the remainder of the population occurs in upland habitat or dry drainages not associated with a well-developed floodplain. Habitat along Arroyo Seco and Kolb creeks includes alluvial sage scrub and Riversidian sage scrub; associated habitat in upland areas includes southern mixed chaparral, chamise chaparral, redshank chaparral, and a coast live oak/southern mixed chaparral ecotone. Additional habitat exists in the vicinity of Vail Lake which could potentially support as yet undiscovered populations of this endangered species.

—PATRICIA GORDON-REEDY, Ogden Environmental and Energy Services Co., San Diego, CA 92121.

CARDAMINE FLEXUOSA With. (BRASSICACEAE).—San Diego Co.: San Diego, Balboa Park, scattered weed in plantings outside and inside Botany Building; several dozen plants seen, 29 January 1997, *M. A. Vincent 7670* (MO, MU, RSA, SD); San Diego Co.: Balboa Park, San Diego Zoo, very common weed in wet area along retaining wall below large aviary; hundreds of plants, 29 January 1997, *M. A. Vincent 7677* & *J. Solomon* (MU, RSA, SD, UC).

Previous knowledge. This European native has been reported for several states in eastern and central North America (R. C. Rollins, 1993, *Cruciferae of Continental North America*, Stanford Univ. Press, Stanford). It is a weed of moist areas and gardens, and is often found in recently planted beds or in pots with potted plants.

Significance. New for California. In *The Jepson Manual* (R. C. Rollins, 1993,

Cardamine, in J. C. Hickman [ed.], The Jepson manual: higher plants of California, Univ. Calif. Press, Berkeley), *C. flexuosa* will key out with *C. pensylvanica*, *C. hirsuta*, and *C. oligosperma*, annuals or biennials from fibrous roots or weak taproots. In California, *C. flexuosa* blooms in December–January, while the other species bloom mid- to late spring. A modified key for these four taxa follows, which would fall under the first lead of couplet 6:

1. Basal lvs 0–few, gen not rosetted, gen deciduous; lower st hairs few or gen 0
 2. Lflets and lobes decurrent on rachis, broadly oval to oblong; sts erect, not flexuous *C. pensylvanica*
 - 2' Lflets and lobes petiolate, oval to orbicular; stems flexuous *C. flexuosa*
- 1' Basal lvs several–many, gen \pm rosetted, persistent; lower st hairs 0 or gen many
 3. Sts 1–many, erect, 5–30 cm, outer 0 or decumbent; fr ≤ 1 mm wide *C. hirsuta*
 - 3' Sts 1–several, erect to ascending, gen > 20 cm; fr 1–2 mm wide *C. oligosperma*

—MICHAEL A. VINCENT, W.S. Turrell Herbarium, Department of Botany, Miami University, Oxford, OH 45056. Vincenma@muohio.edu

GAURA PARVIFLORA L. (ONAGRACEAE).—San Bernardino Co., Montclair, N side of I-10 at W side of Benson Ave., between Central and Mountain Avenues, 34°05.5'N, 117°41'W; T1S R8W S14, alt. 350 m, locally common in dense colonies in a disturbed weedy area, 30 May 1996, A. C. Sanders 18192 (UCR, and to be distributed); 9.5 km N of Crossroads, Colorado River [near Parker Dam], 23 Apr. 1940, A. M. Alexander and L. Kellogg 1213 (RSA).

Previous knowledge. Native to the central U.S. and common west to Arizona. Very scarce in California, previously reported only from “SW” without definite locality by W. L. Wagner (in J. C. Hickman, ed., The Jepson manual: higher plants of California, Univ. of Calif. Press, 1993) and specifically from Orange (P. A. Munz, A flora of Southern California, Univ. of Calif. Press, 1974) and Santa Barbara (C. F. Smith, A flora of Santa Barbara region, California, Santa Barbara Mus. of Nat. Hist., 1976; Munz 1974) counties. Raven and Gregory in their *Gaura* monograph (Mem. Torr. Bot. Club, 23(1):1–96, 1972) did not cite specific collections of this species in the U.S., but did provide a map with small dots indicating collection sites. There are three dots shown in California, one of which doubtless refers to the Crossroads locality cited above. They did see this collection because the RSA duplicate was annotated by them. This earlier dot reference to this collection has evidently been overlooked because neither San Bernardino County nor the California deserts are included within the range of this species in subsequent floristic works (Munz 1974; Wagner 1993).

Significance. First specific records from San Bernardino County and the deserts of California, and first collection since 1956 in California, based on specimens at RSA and UCR. The Crossroads locality may represent the western fringe of the species' natural range, but the coastal slope localities certainly represent introduced populations. The Montclair locality is ca. 25 km NE of a previous locality in Brea, Orange County. This species should be sought at other localities in southern California. It has probably been continuously present since the 1940s but overlooked, despite its 2–3 m stature, because few collectors work on urban weeds.

—ANDREW C. SANDERS, Herbarium, Dept. of Botany and Plant Sciences, University of California, Riverside, CA 92521.

CREPIS TECTORUM L. (ASTERACEAE).—San Bernardino Co., San Bernardino Mtns., Snow Summit Ski area, T2N R1E S28, alt. 2200 m, 20 Sep 1985, *Tim Krantz s.n.* (UCR); Mono Co., Mammoth Lakes, 37°38.8'N, 118°58.8'W, alt. 2470 m, uncommon in one local area on roadside among pines, 26 Sep 1996, *George Helmkamp 1218* (UCR). (Krantz collection determined by John Strother.)

Previous knowledge. Native to Eurasia, previously naturalized in Minnesota and at scattered locations in the Northeast (Gleason, H. and A. Cronquist, *Manual of vascular plants of northeastern United States and adjacent Canada*, 2nd ed., 1991).

Significance. First records for California.

—ANDREW C. SANDERS, Herbarium, Dept. of Botany and Plant Sciences, University of California, Riverside, CA 92521.

REVIEWS

Aspects of the Genesis and Maintenance of Biological Diversity. Edited by MICHAEL E. HOCHBERG, JEAN CLOBERT, and ROBERT BARBAULT. 1996. Oxford University Press, New York. ISBN 0-19-854884-2.

Aspects of the Genesis and Maintenance of Biological Diversity encapsulates 16 presentations from a series of six workshops held in Paris, France, in 1993. The introduction by Robert M. May provides a sobering reminder that only around 1.4 of the 3 to 8 million species on the planet (May's guestimate) have been named and recorded. Realizing that extinction rates in well-documented groups have run a thousand times faster than average background rates, May challenges readers to set priorities on what to save. The three sections of the book define the breath or works, spanning evolutionary biology, population and community ecology, and conservation.

The first two chapters in the first section, "Evolution: Patterns and Processes", begin with clever techniques to fill the gaps in paleontological records to accurately estimate the biodiversity of the past. A smaller group of readers might find Chapter 3 (New Computer Packages for Analyzing Phylogenetic Tree Structure) interesting. Chapter 4, by Nichols and Beaumont, reminds us that "genetic variation within species is one of the most valuable and yet neglected components of biological diversity". Using flies, humans, and grasshoppers as examples, the authors create an eye-opening view of spatial, temporal, and genetic variation. Interesting questions are raised about adaptive polymorphism in heterogeneous environments in Chapter 5, but the answers seemed dependent on future funding.

The second section of the book, "Ecology: From Populations to Communities to Ecosystems", begins with a compelling analogy to Noah's Ark and the urgent need for conservation despite little knowledge of the species we are supposed to save. We are challenged with the fundamental question of whether or not species are interchangeable within functional groups and whether selection favors species that persist with the smallest available nutrient pool. The strongest chapter, by Bryan Shorrocks, is about local diversity: a problem with too many solutions. Using *Drosophila* as a model species, Shorrocks cleverly untangles alpha and beta diversity from fruit stands to a European latitudinal gradient. He provides excellent examples of spatial and temporal diversity, resource selection, and niche and spatial heterogeneity. The book is worth purchasing for the chapter alone. The four following chapters on parasitoid interactions, food web assembly, and nutrient cycling pathways were interesting but less strongly linked to the book's title.

In the overview of the third section, "Large Scale Diversity Patterns and Conservation," Lawton et al. proclaim "It is a disgrace that we have only the haziest notion of the number, distribution, and survival of the species worldwide especially when the rapid growth of human population is the key factor", Chapter 11, by Turner et al., revisits theories from Wallace (1878) and Hutchinson (1959) on the latitudinal gradient of species diversity, only to suggest that the species energy theory has survived our attempts to destroy it. This is followed by the second strongest chapter in the book, by Gaston, on spatial covariance in the species richness of higher taxa. Gaston discusses endemism, rarity, sampling artifacts, issues of spatial scale, spatial autocorrelation, mechanisms, and interactions—all with remarkable clarity and supported with many references. The next three chapters on biodiversity of parasites, taxonomic relatedness, and genetic information seemed out of place in this section. The final chapter, by Thomas, on butterfly metapopulations, provides a strong example of the difficulties in conserving widely dispersed species.

In summary, the book is well written but probably would be more useful to sci-

entists than non-scientists. The book would have benefited from an international discussion on how we can better quantify our planet's biodiversity. The occasional strong chapters make this fairly expensive book an intellectual bargain. However, it is painfully clear from May's challenge in the introduction that far more work is needed to gather and link local, regional, and global information on biodiversity in the face of our planet's sixth wave of extinction.

—THOMAS J. STOHLGREN, Biological Resources Division/USGS (Midcontinent Ecological Science Center) and Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523-1499.

Molecular Genetic Approaches in Conservation. Edited by THOMAS B. SMITH and ROBERT K. WAYNE. 1996. Oxford University Press, New York. 483 pages. \$70.00. ISBN 0-19-509526-X.

The first question a *Madroño* reader is likely to ask about this book is "how many of the 28 chapters are relevant to plant conservation?" The short answer: "disappointingly few." However, hidden in the zoocentric majority, a minority of chapters focus entirely on plants (three to be exact), and several contain material of broad general interest. Although in principle plant and animal conservation biology have much in common, an important distinction arises in molecular genetics: the suitability and availability of polymorphic markers. Most of the conservation genetic methods and case studies presented here exploit the rapidly evolving mitochondrial genome or hypervariable microsatellite markers of animals. These polymorphic and well-characterized markers are extremely informative in measuring diversity and reconstructing population history in animals. In contrast, the mitochondrial genome of plants is slowly evolving and relatively poorly characterized, and therefore difficult to exploit at the levels of interest to conservation biologists. Likewise microsatellite loci, which are already well-characterized in the nuclear genome of many animal species, have been slow to enter the toolbox of plant conservation geneticists. (Microsatellites possess many alleles at each locus and are therefore more powerful in population genetic analyses than dominantly inherited random amplified polymorphic DNA (RAPD), a popular method in plant studies.)

The opening chapter, "An Overview of the Issues", reviews the hierarchical levels (from individual to ecosystem!) at which molecular genetic tools have been applied in conservation biology. Foreshadowing the zoocentricity of subsequent chapters, no botanical examples are given. The next eighteen "methods" chapters cover a variety of techniques, but many of these are not readily transferable to plants due to their reliance on mitochondrial DNA or well-characterized nuclear loci. The chapter on RAPD markers in conservation genetics by Peter Fritsch and Loren Rieseberg is perhaps of the broadest applicability in the book. In fact, it contains the book's only reference to fungi. The well-characterized organellar genome of plants, chloroplast DNA (cpDNA), is the subject of two chapters. Although cpDNA can be effectively used to resolve species-level relationships, it is rarely variable enough to confidently resolve population phylogenies, as is routine for animal mitochondrial DNA. The cpDNA chapters cover traditional restriction site methods and DNA sequencing, respectively. Unfortunately, some of the more innovative applications of PCR to the chloroplast genome (e.g., single-strand conformational polymorphisms and chloroplast simple sequence repeats) are not included. These promising methods do have the potential to resolve population relationships, the hierarchical level of greatest interest in most conservation genetics studies.

The methods section is followed by three "analysis" chapters. They provide good introductions to the issues of estimating effective population size and migration, modeling genetic bottlenecks, and the problems associated with quantifying relatedness from molecular genetic data. All three are based primarily on data from mitochondrial

DNA and/or microsatellites. Most of the above chapters include descriptions of applications of the methods. These many examples provide a good overview of modern conservation genetics. The five following chapters provide additional case studies, covering a variety of vertebrates and one plant, the Pacific yew, *Taxus brevifolia*.

The volume concludes with an excellent and nicely balanced "perspective" chapter by Philip Hedrick. Hedrick reminds us that "many of the critical factors that appear to cause extinctions are not genetic ones" and highlights neglected applications of molecular genetic approaches (e.g., studying loci of adaptive significance). His perspective on the role of molecular genetic data as a complement to ecological and morphological studies in conservation biology is commendable. My overall reaction to the book is that it would be wonderful to see a parallel volume focusing primarily on conservation genetics of plants and fungi. A large amount of excellent work is being done in this area, but all too little of it will be found here.

—AARON LISTON, Department of Botany and Plant Pathology, Oregon State University, Corvallis, OR 97331-2902.

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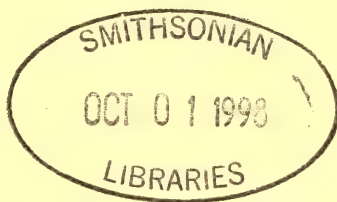
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CHANGING PERCEPTIONS OF PRE-EUROPEAN GRASSLANDS IN CALIFORNIA

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ABSTRACT

The grasslands of California are dominated by non-native annual grasses primarily of Mediterranean origin. Because replacement of native species occurred before extensive botanical study, the original extent and composition of native vegetation is unknown. In 1920, the influential ecologist F. E. Clements concluded that widely scattered patches of perennial bunchgrass were 'relicts' of a once vast perennial grassland. He proposed that the pre-European vegetation of the Central Valley, the valleys of southern California, and many areas of the Coast Ranges were originally dominated by the perennial grass *Nassella pulchra*. Although this hypothesis has become widely accepted, analysis of the data indicates that, especially for central and southern California, this hypothesis is probably incorrect. Clements made a number of mistakes including misidentification of important taxa, over-reliance on his putative 'relicts', misunderstanding of the role of fire in grassland communities, and taking other people's work out of context. Alternative hypotheses have existed for almost as long as Clements' original hypothesis, but these have been generally ignored both by Clements and by many subsequent researchers in the field. There is a growing body of evidence to suggest that many of the areas dominated today by non-native annual grasses may formerly have been dominated by different vegetation types such as oak woodland, chaparral, or coastal scrub.

KEY WORDS: *Nassella pulchra*; *Stipa pulchra*; California grasslands; bunchgrasses; F. E. Clements

Today, large areas of California are dominated by non-native annual grasses primarily of Mediterranean origin. The contemporary temperate grasslands of western North America represent dramatic examples of large scale species replacement due to plant invasions (Mack 1989). In particular, much of central and southern California has been invaded to such an extent and so rapidly by non-native plant species that the original extent and composition of native vegetation will probably never be known with certainty (Keeley 1989; Heady et al. 1992). The native vegetation was destroyed (probably due primarily to overgrazing from domestic livestock) before any significant botanical collections were made (Burcham 1957; Baker 1978). Despite this, the idea that areas that are now dominated by non-native annual grasses were originally dominated by perennial bunchgrasses (primarily *Nassella pulchra*; see Table 1) has been so widely adopted as to be practically axiomatic (e.g., Burcham 1957; Barry 1972; Heady 1977; Fradkin 1995). Grasslands of northwestern

TABLE 1. NOMENCLATURAL CHANGES FOR IMPORTANT SPECIES OF GRASSES IN THE CALIFORNIA GRASSLANDS MENTIONED IN THE TEXT

| Name used in the California literature | Period used | Name used in The Jepson Manual 1993 |
|--|-------------|---|
| <i>Stipa setigera</i> Presl | 1865–1933 | <i>Nassella pulchra</i> sensu lato (sensu lato indicates <i>N. pulchra</i> + <i>N. cernua</i>) |
| <i>Stipa eminens</i> Cav. | 1865–1939 | <i>Nassella lepida</i> (A. Hitchc.) Barkworth |
| <i>Stipa pulchra</i> Hitchc. | 1915–1941 | <i>Nassella pulchra</i> (A. Hitchc.) Barkworth sensu lato |
| <i>Stipa pulchra</i> Hitchc. | 1941–1993 | <i>Nassella pulchra</i> (A. Hitchc.) Barkworth sensu strict. |
| <i>Stipa cernua</i> Stebb. & Love | 1941–1993 | <i>Nassella cernua</i> (Stebb. & Love) Barkworth |
| <i>Stipa lepida</i> Hitchc. | 1915–1993 | <i>Nassella lepida</i> (A. Hitchc.) Barkworth |
| <i>Stipa lemmoni</i> (Vasey) Scribn. | 1901–1993 | <i>Achnatherum lemmonii</i> (Vasey) Barkworth |
| <i>Elymus triticoides</i> Buckl. | 1862–1993 | <i>Leymus triticoides</i> (Buckley) Pilger |
| <i>Festuca megalura</i> Nutt. | 1848–1974 | <i>Vulpia myuros</i> (L.) C. Gmelin |

California form a different community type (Munz and Keck 1950) and are not the subject of this review.

The idea that the pre-European vegetation of the Central Valley, the central and southern Coast Ranges, and valleys of southern California was perennial grassland was first proposed by the influential ecologist F. E. Clements (1920). What was the evidence on which this hypothesis was based? Why has this particular hypothesis enjoyed such acceptance when there have also been a number of alternative hypotheses proposed? In this review, the history of Clements' ideas and how they implicitly and explicitly continue to affect people's views, scientific research, and land management practices are considered. In addition, current thinking on floristic composition and extent of grasslands in California is summarized.

Human understanding improves by building on the work of the past. In order to keep progressing, however, it is sometimes necessary to look back to reevaluate the firmness of the foundation on which we stand. The intellectual history of grasslands in California forms a cautionary tale where force of personality, uncritical acceptance of hypotheses, and weight of scientific authority have sometimes overshadowed data and squelched open debate so important for the progress of science.

A BRIEF TAXONOMIC HISTORY OF *NASSELLA PULCHRA*

To understand the history of thought concerning grasslands in California, it is necessary to review the nomenclatural changes for

the most important native perennial grasses (Table 1). The first floras of California (Bolander 1865; Burt Davy 1901; Abrams 1911; Hitchcock 1912) identified the most common bunchgrass of the Central Valley, the foothills of the Sierra Nevada, and the Coast Ranges as *Stipa setigera*, which was first described from South American collections (Presl 1973). This is the name that Clements used in his early writings (Clements 1920; Clements and Weaver 1924; Weaver and Clements 1929). *Stipa setigera* was a widespread taxon, ranging over California, Oregon, New Mexico, Texas, and South America (Thurber 1880). Although considered variable (Thurber 1880), it was not until 1915 that taxonomists recognized that the name *Stipa setigera* had been misapplied to the California grass (Hitchcock 1915). Based on Presl's original description, it was clear that the name did not apply to the California species (Hitchcock 1915; Presl 1973) and, therefore, Hitchcock described the California bunchgrass as the new species *Stipa pulchra*, restricted to California and Baja California. Even though this new name was used in the floras of California as early as 1923 (Davidson and Moxley 1923; Hitchcock 1923), Clements did not start using it until 1934 (Clements 1934).

In 1941, it was recognized that the taxon *Stipa pulchra* consisted of two distinct types (Stebbins and Love 1941). The form that was predominant in the outer Coast Ranges and the wooded parts of the Sierra Nevada foothills retained the name *Stipa pulchra*, and the other form, occurring primarily in the treeless parts of the inner Coast Ranges, the southern part of the Central Valley and the valleys of southern California was described as *Stipa cernua*. Because Clements' important works on the California grasslands were published before 1941, all references that Clements made to *Stipa setigera* or *Stipa pulchra* did not distinguish these two new types.

A recent taxonomic treatment re-assigns all North American *Stipa* species to several other genera (Barkworth 1990). The most recent California flora accepts this treatment and moves *Stipa pulchra* and *Stipa cernua* into the genus *Nassella* (Barkworth 1993); *Stipa pulchra* becomes *Nassella pulchra* and *Stipa cernua* becomes *Nassella cernua*. This reclassification does not have the ecological ramifications that past nomenclatural changes have had, but it does change the taxonomic relationships of these California bunchgrasses to other North American species formerly considered to belong to the genus *Stipa*.

In this paper, I use species names as they are used by the author of the publication to which I am referring. In parenthesis after the name, I will include my interpretation of the name of the taxon following Barkworth (1993). Because pre-1941 publications did not recognize *Nassella pulchra* as distinct from *Nassella cernua*, I will interpret pre-1941 use of the name *Stipa pulchra* as *Nassella pulchra* sensu lato (s.l.). The name *Stipa setigera* was misapplied and re-

ferred to a number of different taxa; therefore, depending on the context I will either interpret it as *Nassella pulchra* (s.l.), or not attempt interpretation.

ORIGINS OF IDEAS CONCERNING THE PRE-EUROPEAN GRASSLANDS

When Clements first proposed that the pre-European vegetation of the Central Valley had been perennial grassland (Clements 1920), the decline and disappearance of native California bunchgrasses, precipitated by grazing of domestic livestock, had already been documented for parts of northwestern California (Burt Davy 1902). Clements, however, was the first to propose that perennial bunchgrasses had dominated the Central Valley and grassland areas of the central and south Coast Ranges. Although it had been known by at least 1880 that 'grassland' areas of California had come to be dominated by non-native grasses (Thurber 1880), descriptions of the Central Valley from the early 1990s did not distinguish between native and non-native grass taxa, or speculate on the nature of the pre-European vegetation. For example, even though *Avena fatua* (wild oat) was known by grass taxonomists to be non-native, one description by a major figure in California botany states that in the Central Valley "the herbaceous vegetation in aboriginal days grew with utmost rankness, so rank as to excite the wonderment of the first whites, who repeatedly tell of tying wild oats or grasses over the backs of their riding horses" (Jepson 1910).

In 1917, the Executive Committee of the Carnegie Institution of Washington (by which Clements was employed) decided that attention should be given to "grazing problems" (Clements 1917). In the course of this work, Clements studied the vegetation of many western states, including California (Clements 1917; Clements 1918; Clements 1919). This resulted in the first published descriptions of the presumed pre-European vegetation of the California Central Valley (Clements 1920).

Clements recognized that the original vegetation had long since disappeared, so he attempted to reconstruct the pre-European condition by searching out 'relict' patches of grasses. After deciding that the original dominants had been *Stipa setigera* (*Nassella pulchra* s.l.) and *Stipa eminens* (*Nassella lepida*), he searched for 'relict' patches to determine the extent of the original grassland. As a result, he concluded that these grasses had dominated the Central Valley from Bakersfield to Mount Shasta and from the foothills of the Sierra Nevada and Cascade mountains, through much of the Coast Ranges (Clements 1920).

Describing the 'grasslands' of California, Clements said that "the native bunch grasses once occupied all of the Great Valley of California as well as the valleys and lower foothills of the Coast and

Cross ranges and of the Sierra Nevada" (Weaver and Clements 1929). Nevertheless, such statements must be understood as describing what he perceived to be the potential vegetation that would develop in a given area based on the climate (Clements 1916). Clements recognized that the dominant species in an area at a given time would depend on hydrology and soil type. For example, he states that in parts of the San Joaquin, Salinas, and other valleys, species other than *Nassella pulchra* s.l., such as *Elymus triticoides* (= *Leymus triticoides*), formed extensive communities. He also described a "great complex of tule marshes" in the Sacramento and San Joaquin river delta (Clements and Shelford 1939).

WHAT WAS CLEMENTS' EVIDENCE?

By the time Clements became interested in what are now non-native-annual-dominated grasslands in California, the vegetation of these areas had been so extensively altered that the pre-European condition was unrecognizable. In his words, "the valleys and hills of California are to-day covered with a continuous mantle composed of annual species. . . . These have seemingly replaced the native perennials . . . so completely as to have produced grave doubt as to the composition of the original climax" (Clements 1934). Despite this, Clements harbored no doubt that he had correctly ascertained the pre-European vegetation: the "search for relict areas . . . has been so successful that it is now possible to determine its original area and composition . . ." (Weaver and Clements 1929). What was the evidence that Clements found so convincing?

In his first publication on the topic, Clements stated that "it was confirmed in 1917 . . . that *Stipa setigera* (*Nassella pulchra* s.l.) and *S. eminens* (*Nassella lepida*) were the original bunch-grasses of California" (Clements 1920), but he did not present data on which this conclusion was based. He continued "the [Californian] part of the [Pacific grasslands] is much more fragmentary, so much so in fact that it has had to be reconstructed from widely scattered relicts." Somehow Clements had convinced himself that scattered patches of *Stipa setigera* (*Nassella pulchra* s.l.) were relicts of a once vast association. For example, he used the occurrence of a few individuals of *Stipa setigera* (*Nassella pulchra* s.l.) growing among *Opuntia* near Banning, California, as evidence that "extensive areas" were once bunchgrass dominated (Clements 1934). He even used the occurrence of bunchgrasses in the deserts of California to conclude that these areas had once been bunchgrass prairie that had been transformed due to climatic changes (Clements 1920).

The primary observational evidence that Clements relied on was the vegetation along railroad right-of-ways in the Central Valley (Clements 1920). Along the tracks he observed "many hundred

miles of a nearly continuous consociation of *Stipa pulchra* (*Nassella pulchra* s.l.)" that was "often remarkable in purity and extent" (Clements 1934). Clements wrote that "it was especial good fortune to record these extensive relicts and then to have seen them reduced to patches here and there, as it . . . confirms the other evidence to the effect that grassland was the original great climax of California . . ." (Clements 1934).

Although Clements mentions "other evidence", it is not clear to what he was referring. To determine the original extent of the perennial grasslands he made a "special search . . . for relict patches of *Stipa*" (Clements 1920), but there is no indication in any of his writings how he determined that these patches were relicts. Clements also maintained that he supplemented this search with "information from collections, ranges, the statements of early settlers, and the accounts of earlier collectors and explorers" (Clements 1920), but the only source he cites is a report by J. Burt Davy that dealt with northwestern California and entirely different species of grasses (Burt Davy 1902).

Many years later, Clements wrote that his conclusions were reinforced by field and garden studies although, again, he did not give any more information (Clements and Shelford 1939). I have been unable to find evidence for any experiments that Clements might have performed that could have supported his claims. In his book *Experimental Vegetation* (Clements and Weaver 1924), Clements reports planting *Stipa setigera* (*Nassella pulchra* s.l.) at a number of plots in the Midwest with the result that the California grass was always killed by winter weather. Clements never comments on the relevancy of this finding for determinations of the pre-European vegetation of California. I have found one other reference to a set of enclosure experiments performed at Palo Alto by a colleague of Clements, but the results never seem to have been published (Vestal 1929).

So we are left with the only evidence being widely scattered patches of *Stipa setigera* (*Nassella pulchra* s.l.) in the 'grassland' areas of California and fairly pure communities of this grass along trackways in the Central Valley. Clements did provide one major clue into his thinking, however, when he stated "The constant examination of fenced right-of-ways . . . has confirmed the *theoretical assumption* that this was formerly a vast *Stipa* association" (Clements 1920) (emphasis added). Fortunately, Clements has provided enough information in his writings to elucidate this suggestive statement.

CLIMAX THEORY AND THE CALIFORNIA GRASSLANDS

To understand how Clements came to the conclusion that *Stipa setigera* (*Nassella pulchra* s.l.) was the original dominant of Cali-

for California grasslands, it is necessary to understand the conceptual framework he had developed for vegetation analysis and the problems that he was interested in addressing. In his influential 1905 work *Research Methods in Ecology*, Clements laid the foundations of the theory that was to govern his career and the entire field of ecology in the United States for many years. He was looking for a "guiding principle" or "logical superstructure" on which to base the science of ecology, and, in his view, this principle was the relationship between "habitat" and plant. To Clements, this was a direct cause-and-effect relationship in which a "habitat" (i.e., various environmental factors) is the cause and plants and plant communities are the effects (Clements 1905). One of the primary research goals to which Clements applied his theory was in development of an explanation for continental-scale vegetation patterns of North America.

With his next major publication in 1916, Clements developed his ecological theory to the point that he viewed every successional sequence as ending in a definite, stabilized state called a formation or a climax (Clements 1916). His theory did allow for situations where conditions might greatly slow a successional sequence, but in general he viewed succession as the development and reproduction of a complex organism, and, as such, every successional sequence always eventually ended in a single, determinate state controlled by climate. Using his climax theory, Clements classified the vegetation of North America into 19 climaxes. He had not yet considered the 'grasslands' of California or the Palouse Prairie of the Pacific Northwest, but he concluded that the major grasslands of the Great Plains were one climax with three major plant associations.

By the publication of *Plant Indicators* in 1920, Clements no longer viewed his climax theory as a useful model nor as a hypothesis requiring testing, but as a fundamental principle:

... it is ... necessary to recognize that the successional areas in the great grassland formation, for example, are an integral part of the climax, however much they may differ from it. *Whatever seems inconsistent in this is apparent and not real*, since it is a matter of common knowledge that the same organism may appear in two or more unlike forms, such as the seedling and adult plant ... (Clements 1920).

He continued by stating the criteria by which climaxes could be 'objectively' recognized: (1) dominant plants must all belong to the same vegetation-form, (2) one or more of the dominant species must range throughout the formation as a dominant, (3) the majority of the dominant genera extended throughout the formation, (4) subclimax dominants give way to climax dominants through succession. In addition, it was a commonly accepted idea, which Clements had already stated in 1916, that, although annuals might dominate an

area in an early successional stage, they would typically yield to perennials in later stages (e.g., Clements 1916; Sampson and Chase 1927; Bews 1929; Piemeisel and Lawson 1937).

So consider Clements' conceptual framework and the issues in which he was interested when he came to California for his expeditions of 1917, 1918, and 1919. He was taking a large-scale, long-term view of community classification (Bartolome 1989). Following in the footsteps of other authors (Merriam 1898; Hall and Grinnell 1919), Clements wanted to understand large-scale vegetation patterns. In this pursuit, Clements was inclined toward a classification scheme with a few large categories rather than many small categories. He had already decided that the Great Plains were a single climax formation dominated by the genera *Stipa*, *Agropyrum* (= *Agropyron* sensu lato), *Bouteloua*, *Aristida*, and *Koeleria*. Based on the work of Weaver (1917), Clements concluded that the Palouse Prairie of the Pacific Northwest was part of the same climax. He had thus included all the grassland areas of North America in one large climax formation by the time he arrived in California. Based on the criteria he had laid down for climaxes, if the 'grasslands' of California were to be included in this climax, the original dominants had to be perennial grasses, belonging to one of the five genera that he had already delineated. Thus, when he arrived, he was predisposed to look for particular taxa. Although most native grasses were scarce, the perennial bunchgrass that he identified as *Stipa setigera* (*Nassella pulchra* s.l.) was common (Bolander 1865), and was the only one listed by other authors as an indicator species for certain climate zones in the state (Hall and Grinnell 1919). Guided by his theory, Clements knew a priori what he was looking for, and he found it.

Clements' hypotheses that (1) the California grasslands were dominated by *Stipa setigera* (*Nassella pulchra* s.l.) and (2) were part of a larger North American grassland climax would not have satisfied his own criteria for climax (particularly 2) if his putative dominant occurred only in California. However, because of a taxonomic mistake, he believed that the dominant grass in California was the widespread *Stipa setigera* instead of a California species with a much more restricted range. As already noted, the taxon *Stipa setigera* was considered to be distributed from San Diego County, northward to Oregon, eastward to New Mexico and Texas, and southward into South America (Thurber 1880; Hitchcock 1912). In fact, Clements used the occurrence of *Stipa setigera* and *Stipa emmens* (*Nassella lepida*) at high elevations of the mixed prairies in Texas and Arizona as evidence for the grassland climax (Clements and Weaver 1924). Clements assumed that the pre-European vegetation of those portions of California now dominated by introduced annual grasses formerly was native grassland. Then, in order to

group this 'grassland' with the other grasslands of North America, he needed the original dominants to be perennial grasses of certain genera. The occurrence of *Stipa* in California was the final piece of the puzzle that he needed:

The conclusion that the grassland is a single great climax formation is based in the first place on the fact that the three most important dominants, *Stipa*, *Agropyrum*, and *Bouteloua*, extend over most of the area, and one or the other is present in practically every association in it. This would seem the most conclusive evidence possible, short of actual vegetation experiments, that the grassland is a climatic vegetation unit (Clements 1920).

Clements was aware of the criticism that he was proposing the same climax for areas of California with vastly different amounts of rainfall. This criticism has, in fact, been used many times to argue against Clements' grassland hypothesis (e.g., Twisselmann 1967). His answer was that climate can only be recognized by vegetation: "No matter how complete his equipment of meteorological instruments, the ecologist must learn to subordinate his determination of climate to that of the plant . . ." (Clements 1920). Thus, he concluded that if dry areas such as the San Joaquin or Antelope Valley had bunchgrasses, then the climate was the same in these areas as in other areas with greater rainfall that supported bunchgrasses (Clements and Shelford 1939). The logic that he seemed to follow was that if two different areas both had bunchgrasses, then the climates were the same. If the climates were the same, then the climax vegetation was the same.

THE ACCEPTANCE OF THE PARADIGM

After Clements proposed his California grassland hypothesis in 1920, his ideas became so widely accepted as to form a standard paradigm. This paradigm consisted of two elements: (1) ideas concerning the composition and distribution of 'California bunchgrass grassland' and (2) the grouping of 'grasslands' in the entire Central Valley, the central and southern Coast Ranges, and southern California into a single community type.

In the almost eight decades since Clements first published his hypotheses, they have become widely accepted by researchers from a number of different areas. A major impetus to this acceptance was the publication in 1929 of Clements' textbook on ecology (co-authored with Weaver), that included his hypotheses on California vegetation (Weaver and Clements 1929). Thus began a trend in which his hypotheses were incorporated into textbooks in general ecology (e.g., Weaver and Clements 1938; Clements and Shelford 1939;

Oosting 1948; Oosting 1956; Shelford 1963; Barbour et al. 1987), general texts on grass taxonomy (e.g., Bews 1929; Gould 1968; Gould and Shaw 1983), range management (e.g., Stoddard et al. 1975), and fire ecology (e.g., Wright and Bailey 1982). The idea was reiterated in studies of California vegetation published in prestigious scientific journals such as *Ecology* (e.g., Klyver 1931; Clark 1937; Bentley and Talbot 1948). It was adopted by researchers at the United States Department of Agriculture (e.g., Shantz and Zon 1924; McArdle and Costello 1936; Piemeisel and Lawson 1937), various California state agencies (e.g., Burcham 1957; Barry 1972), and the University of California Agricultural Experiment Station (e.g., Robbins 1940; Sampson et al. 1951). The dominance of *Stipa pulchra* (*Nassella pulchra*) was proclaimed in standard floras of California (e.g., Munz 1959, 1974), specialized floras of California grasses (e.g., Crampton 1974), and general treatises on California vegetation (e.g., Barbour and Major 1977). It was incorporated into general geographical treatments of California (e.g., Hornbeck 1983; Miller and Hyslop 1983), general treatments of the vegetation of North America (e.g., Kuchler 1964; Sims 1988), and treatments on grasslands of the world (e.g., Heady et al. 1992).

A few of these publications have been particularly influential owing to timing, place of publication, or nature of the publication. For example, the adoption of Clements' views with essentially no modification for the *Atlas of American Agriculture* in 1924 (Shantz and Zon 1924) was the first step in cementing Clements' hypotheses in the scientific community. This was the citation that got the California grassland hypothesis into textbooks (e.g., Bews 1929) and U.S. Senate documents (e.g., McArdle and Costello 1936). The next particularly influential publication was a paper in *Hilgardia* by Beetle (1947). This often-cited paper reinforced the idea with a number of range maps that show perennial grass species covering the entire Central Valley. One review published in 1957 (Burcham 1957) was so influential that many subsequent authors relied on it as a primary source (e.g., Gould 1968; Barry 1972; Wright and Bailey 1982; Gould and Shaw 1983). This review also served to introduce the California grassland hypothesis into many popular accounts of the natural history of California (e.g., Dasmann 1965; Bakker 1971; Barry 1972; Bakker 1984; Dasmann 1988; Fradkin 1995). Finally, the publication that firmly cemented the California grassland hypothesis in the minds of both scientists and the public, because it serves as a primary starting point for the study of California vegetation, was the treatment by Heady in 1977 (reprinted in 1988) in *Terrestrial Vegetation of California* (Heady 1977). Heady wrote "*Stipa pulchra* [*Nassella pulchra*], beyond all doubt, dominated the valley grassland."

Clements' ideas have proven to be important in another respect.

His system of vegetation classification was based on observations of plants in the field and was a great improvement over climatically determined life-zones in common use at the time (Merriam 1898; Hall and Grinnell 1919; Jepson 1925). These systems, for example, placed the entire floor of the Central Valley and the California portion of the Sonoran Desert in the same category. Although Clements' hierarchical system could allow for intra-regional differentiation, because of his emphasis on the highest level of classification, he did not look for differences in communities from north to south or from coast to interior. In the decades following Clements, researchers either used Clements views in their descriptions of the California 'grasslands' (e.g., Shantz and Zon 1924; Piemeisel and Lawson 1937), or simply described the vegetation as "grass" and left it at that (e.g., Shreve 1927; Wieslander and Jensen 1946; Jensen 1947). Even earlier researchers who recognized that the north coast of California was composed of different species and should not be classified in the same vegetation type as the Central Valley did not differentiate plant communities within the Central Valley or in southern California (e.g., Clark 1937).

The defining paper in California plant community classification was that of Munz and Keck in 1949, with an addition in 1950 (Munz and Keck 1949; Munz and Keck 1950). In their community descriptions, they combined the ideas of scientists such as Jensen (1947), who recognized a single vegetation type termed "grass", with the floristic ideas of Clements (1920) and classified all the 'grassland' areas of the Central Valley, the Inner Coast Ranges, and of southern California as bunchgrass grassland ("Valley Grassland") dominated by *Stipa pulchra* (*Nassella pulchra*). In addition, they recognized another, more mesic, grassland community for northern coastal California (that they termed "Coastal Prairie").

This two-type classification was adopted in Munz's (1959) widely used flora and, with little modification, became the standard description of California 'grasslands' (e.g., Burcham 1957; Kuchler 1964; Barry 1972; Ornduff 1974; Cheatham and Haller 1975; Holland and Keil 1990). This blanket acceptance persisted despite the fact that rainfall varies over this area by more than 800 mm (Bentley and Talbot 1948), and even though there was a known difference in species distribution and abundance between the northern and southern Central Valley, and between the Central Valley and the Coast Ranges (Stebbins and Love 1941; Beetle 1947; Burcham 1957).

ALTERNATIVE HYPOTHESES TO THE BUNCHGRASS PRAIRIE

Because of the widespread acceptance of Clements' hypothesis, it might be assumed that there were no competing hypotheses; however, this is not the case. In fact, there are several alternatives that

date back almost as far as the publication of Clements' original idea in 1920. The first major alternative to Clements' grassland hypothesis was published only two years after Clements' hypothesis (Cooper 1922). In this model, the area of California with 250–760 mm of rainfall per year was dominated by sclerophyllous shrubs. Thus, the pre-European vegetation of large parts of the Coast Ranges, the foothills of the Sierra Nevada, and even the northern end of the Central Valley was proposed to have been chaparral. Areas with less than 250 mm of rainfall were considered deserts. It is noteworthy that this hypothesis was first derived under the paradigm of Clementsian climax theory and used exactly the same types of observations that Clements used: assumed relict patches of vegetation and eyewitness reports. The difference is that the second hypothesis recognized the possibility that areas currently dominated by grasses may, at one time, have been dominated by other vegetation types.

This hypothesis was extended by a number of researchers over the next several decades (Bauer 1930; Sampson 1944; Wells 1962; Naveh 1967; Keeley 1989). Also using assumed relicts as evidence, Bauer argued that in addition to the areas named by Cooper, much of the southern San Joaquin Valley had also been chaparral and not grassland (Bauer 1930). Others have come to similar conclusions. For example, in an extensive study of the relationship between vegetation type, substrate, and disturbance, Wells (1962) concluded that the original vegetation of the San Luis Obispo area was broad-sclerophyll forest on all types of substratum. In his view, anthropogenically caused fires (starting with native Americans and continuing with European settlers) and grazing eventually destroyed this forest, leading to the currently observed mosaic of grassland, shrubland, and forest. Wells predicted that continued destruction of the original forest would lead to the increased popularity of the grassland climax hypothesis: "... if the present conditions continue, one can hardly doubt that the hypothesis of a grassland climax will gain ascendancy as the contrary evidence disappears."

Researchers who explicitly rejected Clements' climax theory also came to the conclusion that modern non-native-annual-dominated grasslands had been dominated by chaparral. In a comparison of California with areas of the Mediterranean Basin, Naveh (1967) came to the same conclusion as Cooper. He concludes that "the probability of a climatic bunchgrass climax ... seems very low." Recently, a number of scientists have championed the idea that many areas of California 'grasslands' were once dominated by chaparral (Zedler et al. 1983; Freudenberger et al. 1987; Hunter and Horenstein 1992; Keeley 1993).

The second major alternative hypothesis was proposed by Jepson, who suggested that the pre-European vegetation of the Central Valley was dominated by annual plants (Jepson 1925). Research at the

San Joaquin Experimental Range (Talbot et al. 1939; Talbot and Biswell 1942) indicated that 'native' annual grasses were an important part of the flora. This caused some researchers (Bentley and Talbot 1948) to conclude that annuals may have dominated some areas of the foothill grasslands (at the time, *Festuca megalura* (= *Vulpia myuros*), was thought to be a native annual), and even researchers who still accepted Clements' hypothesis admitted that the California 'grasslands' were unique in the number of native annuals (Beetle 1947). Research into the climatic conditions that favor annual plants over perennials has also tended to support the dominant role of annual plants (though not necessarily grasses) in some areas (Blumler 1984; Blumler 1992; Paula Schiffman in press).

The recognition that California has many native annual species has led to a number of variants of this hypothesis. For example, one proposal is that perennial grasses were the original dominants along the coast where conditions are most favorable for them, and native annuals were dominant in areas such as the lower foothills of the western slope of the Sierra Nevada (Biswell 1956). Another idea is that the floor of the Central Valley was a largely native annual grassland, with desert at the extreme southern end, but that at higher elevations perennial grasses were dominant (Twisselmann 1967; Frenkel 1970; Baker 1978). Others hypothesized that the annual vegetation on the floor of the valley was composed of herbaceous plants other than grasses (Piemeisel and Lawson 1937; Hoover 1970). Based partly on research into the interactions between the giant kangaroo rat (*Dipodomys ingens* Merriam) and *Nassella*, this is also the conclusion reached for parts of the Carrizo Plain in San Luis Obispo County (Schiffman 1994; Schiffman in press).

The third major counter-hypothesis is that vegetation is not controlled primarily by climate, but by soil characteristics. Thus, grasslands were found on deep soils, with different vegetation types on other soils (Shreve 1927). This hypothesis was supported by Robinson (1968, 1971) and independently by Keeley (1993), who concluded that *Stipa pulchra* (*Nassella pulchra* s.l.) was dominant in the Central Valley grassland and in the foothills of the Coast Ranges only on deep agricultural-type soils or heavy soils high in mineral nutrients. Well-drained sandy soils and those poor in mineral nutrients probably never supported such associations.

A CRITICAL ANALYSIS OF CLEMENTS' DATA

There are a number of important problems with the evidence used to support Clements' hypothesis. The first is taxonomy. The common native bunchgrass of California was originally identified as the widespread *Stipa setigera*. In part, Clements used the distribution of this species to support his idea of a grassland climax over this area.

When *Stipa pulchra* (*Nassella pulchra* s.l.) in California was recognized as a different species, this line of evidence was no longer valid. Clements, however, never mentioned this in any of his later publications. He simply replaced one name with another, without any discussion of the consequences that this taxonomic change had for his ecological theory or his California grassland hypothesis.

The second problem is that Clements considered roadsides and trackways to be undisturbed relict vegetation. In 1932, Clements' close colleague, Weaver, directly attacked using roadside vegetation to draw conclusions about the vegetation of larger areas (Weaver and Fitzpatrick 1932). Weaver concluded: "Along roadways and in right-of-ways certain species make a good showing. Their conspicuousness and abundance are often such as to lead one to believe that they are really important in the prairie proper In many cases these are found only sparingly, if at all, in the prairies" This was two years before Clements wrote his 1934 paper discussing the fundamental utility of roadside vegetation. There is no doubt that Clements knew of this criticism (the paper is cited in one of his books (Weaver and Clements 1938)), but Clements never addressed the issue. Furthermore, the *Stipa* (*Nassella*) communities along the trackways near Fresno that Clements used as the prime example of the pristine vegetation in California were burned every year (Biswell 1956), and therefore were not undisturbed relict patches.

The third problem concerns a misunderstanding of the role of fire in *Nassella* communities. Clements recognized that these communities were being burned, but he thought this destroyed them (Clements 1934). It is now known that fire often promotes *Nassella* and probably resulted in an increase in density (Sampson 1944; Jones and Love 1945; Biswell 1956; Ahmed 1983).

Finally, Clements took other people's work out of context. In his 1920 publication, Clements cites the work of Burtt Davy (1902) to support his contention that native *Stipa* species were the pre-European grasses of the Central Valley. Burtt Davy, however, was discussing only extreme northwest California, not the Coast Ranges nor the Central Valley, and he was referring to an entirely different species of *Stipa* (*Stipa lemmoni* = *Achnatherum lemmonii*)!

THE VIEW TODAY

We return to the question as to the nature of the pre-European vegetation that is dominated today by introduced annual grasses. In many areas, there is little question that the pre-European vegetation was oak forest, chaparral, or coastal sage scrub, as California has a well-documented history of shrub-clearing as a 'range improvement' practice (e.g., Sampson 1944; Jones and Love 1945; Arnold et al. 1951; Wells 1962; McKell et al. 1965; Zedler et al. 1983; Freuden-

berger et al. 1987; Huenneke 1989; Hunter and Horenstein 1992; Keeley 1993). For areas in northern California and in the northern part of the Central Valley, there are reliable eyewitness accounts of the existence of bunchgrasses (Burcham 1957; Wester 1981). In the way of physical evidence, microfossils in the form of silica bodies (opal phytoliths) most probably from *Nassella pulchra* have been found in areas of northern California that are today dominated by introduced annual grasses (Bartolome et al. 1986). Although strong evidence for the occurrence of *Nassella* in these areas, presence of these silica bodies does not preclude the possibility that the original vegetation was savanna or woodland.

Nassella pulchra is the most common native perennial grass today, and it is probable that in many areas it may have increased due to anthropogenic disturbances (Bartolome and Gemmill 1981). For example, *Nassella pulchra* is known to colonize road cuts (Clements 1934; Heady et al. 1992), and it is promoted by fire (Sampson 1944; Jones and Love 1945; Wells 1962; Ahmed 1983). Frequent burning can even be used to help produce monocultures of *Nassella pulchra* (Paul Kephardt, personal communication).

What can be concluded about the pre-European vegetation of the Central Valley? Eyewitness accounts from the early 1800s of the central and southern Central Valley appear inconclusive (Heady 1977). Wester has pointed out that most of the early accounts that mention bunchgrasses are from northern coastal locations or the Coast Ranges. Spanish and early Anglo-American accounts of the Central Valley (before serious overgrazing had occurred) tell of very sparse vegetation and no bunchgrasses. This might indicate that much of the southern Central Valley supported annual species. There are early accounts of bunchgrasses, but these descriptions confine bunchgrasses to the northeast portion of the San Joaquin Valley (Wester 1981).

There has never been any question that there were large areas of riparian vegetation and fresh water marshes around rivers (Shantz and Zon 1924; Clements and Shelford 1939; Burcham 1957; Heady 1977; Heady et al. 1992) and large vernal pool complexes on the eastern side of the Central Valley (Burcham 1957; Heady 1977; Heady et al. 1992). In addition, it is now generally agreed that areas of the valley floor, particularly in the southern Central Valley, are semi-desert (Twisselmann 1967; Menke 1989) and were originally dominated by some kind of desert scrub vegetation (Shantz and Zon 1924; Piemeisel and Lawson 1937; Burcham 1957; Twisselmann 1967; Heady 1977). This agrees with experimental work that found that the climate of the Kern Basin was too dry for perennial grasses (Jones and Love 1945).

Contemporary reviewers (Keeley 1989; Heady et al. 1992; Holland and Keil 1995) have tended to be much more careful in their

claims than those writing during the first eight decades of the century. The most recent reviews have tended to reverse the view of vast, relatively homogeneous perennial grasslands, and portray the pre-European California 'grassland' vegetation as a complex mosaic of different herbaceous communities with the particular species composition depending on climate and local conditions. Nobody has yet declared that perennial grasslands were unimportant components of California's vegetation, but there has been an increasing recognition that there are species differences and changes in relative abundance of perennials and annuals between north and south, Coast Ranges and Central Valley, and within the Central Valley depending on specific site conditions. With the recognition that *Vulpia myuros* is not native, as was once thought (Lonard and Gould 1974), many researchers have proposed that annual forbs filled the interstitial spaces of perennial grasslands, because there seem to be few common graminaceous candidates other than *Vulpia myuros* (Crampton 1974; Keeley 1989; Heady et al. 1992).

We will never know with certainty what the pre-European vegetation of large portions of California looked like. Nonetheless, the evidence strongly indicates that the poetic images of *Nassella*-dominated bunchgrass prairie blanketing vast expanses of the Central Valley and other 'grassland' areas of California are not accurate. There probably were stands of bunchgrasses in the northern Central Valley on rich soils and in some areas of the Coast Ranges. The central and southern Central Valley was probably a complex mosaic of plant communities with bunchgrasses becoming less and less important toward the south. In these areas, communities of annuals probably dominated, with forbs being more important than grasses. Finally at the extreme southern end of the Central Valley, a desert scrub vegetation probably dominated.

THE LEGACY OF CLEMENTS

Clements' California grassland hypothesis did not become the standard paradigm because it was based on the most convincing evidence or because there were no credible alternatives. The primary reason it became so widespread was because Clements was one of the most influential ecologists of the twentieth century. Clements' tremendous influence was due in great part to his voluminous writings on virtually every topic in ecology (Hagen 1992). In addition to research papers and monographs, Clements wrote or strongly influenced the standard textbooks of ecology for at least 35 years (Weaver and Clements 1929; Clements and Shelford 1939; Oosting 1956; Shelford 1963).

Clements continually ignored criticism or alternative hypotheses in his writings. For example, in other contexts, Clements cited Co-

per's monograph that contains a directly contrary hypothesis concerning the California grasslands (Cooper 1922) but never addressed Cooper's ideas concerning that hypothesis. Because of Clement's silence concerning alternative hypotheses, much of the existing dissent was known only to a limited group of specialists.

Clements does not bear sole responsibility for the lack of recognition accorded alternative hypotheses. His paradigm was also perpetuated because important reviews downplayed alternatives (Burcham 1957; Heady 1977). Reviews can continue to perpetuate ideas after they are considered by other specialists in the field to be in doubt or even to be outdated.

Clements' legacy in ideas pertaining to grasslands in California has been far reaching. Today, we are still trying to shake off his influence. For example, the emphasis on *Nassella pulchra* as the dominant of large areas of 'grasslands' in California has led to concentration ecological research and restoration and management efforts on this species, at the expense of others. More studies, such as that of Dennis (1989), that compare the different effects of management regimes on a variety of native grasses are needed.

Because of the Clementsian paradigm that there were few north/south or coastal/interior differences in California grass communities, there has been a lack of appreciation for these differences. Management prescriptions developed in Jepson Prairie in northern California (Menke 1992) may not be appropriate for 'grassland' areas of southern California. It is only very recently that there has been a growing recognition that regional differences in 'grassland' communities, as well as ecotypic variation in native species, might be important ecologically (Huenneke 1989; Keeley 1989; Huntsinger et al. 1996). Community classifications that include more vegetation types may help in this regard (Thorne 1976; Holland 1986; Magney 1992), as may a more fine-scale floristic-based approach (Sawyer and Keeler-Wolf 1995).

Recognition that areas which today are dominated by annual grasses formerly may have been dominated by a different vegetation type (e.g., oak woodland, chaparral, or coastal sage scrub) can benefit restoration programs (Keeley 1993). With this recognition, potential sites for 'grassland' restoration can be chosen to allow true restoration, rather than type conversion. Also, an increase in shrubs in some areas may not be a call to action, because this may actually be recovery from past disturbance rather than an invasion of an endangered grassland community (e.g., McBride and Heady 1968).

Although simplification for popular publications is sometimes necessary and desirable, oversimplification is not. Popular references abound (e.g., Dasmann 1965; Barry 1972; Bakker 1984; Dasmann 1988; Edwards 1992; Fradkin 1995) that simply perpetuate Clements' ideas and do not incorporate the latest thinking. Lack of

appreciation of the diversity of California's plant communities can lead to poor decisions when questions of funding for basic research, conservation, or management are concerned. It is important that ecologists begin to convey to the public the complexity and diversity, rather than the homogeneity, of the vegetation.

The foregoing history is a reminder of the potential dangers of forcing facts to fit a hypothesis. It is true that, for observations to contribute to scientific knowledge, they must be influenced by theory; without any kind of conceptual framework with which to understand what we see, observations will be unintelligible (Kosso 1992). Nevertheless, hypotheses can also become traps if one forgets that the guiding hypothesis is only that, and is itself open to modification or replacement. Clementsian climax theory was a great advance for its time, but its widespread acceptance eventually hindered advance in ecology, conservation, and management. When Clements came to California, he used his theory to understand what he saw, but he, and many others, neglected to critically evaluate these views in light of all the evidence.

Because the observations of any individual are necessarily influenced by that person's preconceived notions, objectivity can only be achieved by subjecting ideas to the diverse community of scientists for debate (Pickett et al. 1994). Weight of authority should have no place in acceptance of scientific theories. Clements used his position as one of the preeminent ecologists of his day to promote his ideas. He ignored alternatives, and many other scientists chose not to discuss dissenting ideas. The consequences of this lack of open debate are still with us today.

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ALLELIC VARIATION IN THE AMPHITROPICAL DISJUNCT *LYCURUS SETOSUS* (POACEAE: MUHLENBERGIIAE)

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ABSTRACT

Lycurus consists of three species, all with paired, single-flowered spikelets (the lower is short pedicellate and usually staminate, the upper long pedicellate and perfect). *Lycurus setosus* occurs in the southwestern USA, northern Mexico, northwestern Argentina, and Bolivia. Allozyme data were used to evaluate genetic diversity within and among populations of this amphitropical disjunct species. Electrophoretic examination of 18 putative enzyme loci in 13 populations revealed high levels of genetic variation (P ranging from 0.43 to 0.79; H from 0.31 to 0.62) and high levels of genetic diversity (F ranging from -0.38 to -1.00). All populations possess high levels of heterogeneity (F_{is} approaching -1 , mean of -0.723) and exhibit lower levels of genetic fixation among populations (F_{ST} mean of 0.256). A comparison of genetic identity values among populations from North and South America indicates that the genetic variation is greater ($I = 0.89$) in North America than in South America ($I = 0.94$), and populations from South America lack six alleles found in the North American populations. There was one unique allele found in populations from South America. It seems likely that *Lycurus setosus* has recently dispersed to South America because the populations there contain less genetic variation.

RESUMEN

Lycurus consiste en tres especies, todas con espiguillas dispuestas en pares, flosculo único (el basal brevemente pedicelado y usualmente estaminado, y el distal largamente pedicelado y perfecta). *Lycurus setosus* habita en el suroeste de Estados Unidos, norte de México, noreste de Argentina y Bolivia. Mediante el análisis de alozimas se evaluó la diversidad genética dentro y entre poblaciones de esta especie disjuntiva anfitropical. El exámen electroforético de 18 loci putativos enzimáticos en 13 poblaciones, reveló altos niveles de variación genética (P varía de 0.43 a 0.79; H varía de 0.31 a 0.62) y altos niveles de diversidad genética (F varía de -0.38 a -1.00). Todas las poblaciones poseen altos niveles de heterogeneidad dentro de las mismas poblaciones (F_{is} cerca -1 , media de -0.723) y exhiben bajos niveles de fijación genética entre poblaciones (F_{ST} media de 0.256). Una comparación de valores de identidad genética entre poblaciones de Norte y Sur América indican que la variación genética es mayor ($I = 0.89$) en Norte América que en Sur América ($I = 0.94$), y poblaciones de Sur América carecen de seis alelos encontrados en poblaciones de Norte América. Se halló un único alelo en poblaciones de Sur Americanas. Probablemente, *Lycurus setosus* ha sido recientemente dispersado hacia Sur América porque esta poblaciones contienen menos variación genética.

Lycurus Kunth consists of three species restricted to the New World: *L. phalaroides* Kunth, *L. phleoides* Kunth, and *L. setosus* (Nutt.) C. Reeder. The amphitropical disjunct, *Lycurus setosus*, occurs in the southwestern U.S. and northern Mexico, and again in northwestern Argentina and Bolivia. This species was originally described by Nuttall (1848) from plants collected in the vicinity of Santa Fe, New Mexico, as a distinct genus *Pleopogon setosum* Nutt. Beal (1896) recognized this taxon as *Lycurus phleoides* Kunth var. *glaucifolius* Beal. Later authors placed this species as a synonym of *L. phleoides* (Hitchcock 1913, 1937, 1939). It was not until C. Reeder (1985) revised *Lycurus* that we came to recognize *L. setosus* as a third species in the genus.

The genus is characterized by having paired, single-flowered spikelets; the lower short, pedicellate and usually staminate, occasionally sterile or perfect, the upper long pedicellate and perfect (Peterson et al. 1997). The first glume is 2- or 3-nerved with two awns, 3–7 mm long and the lemma is 3-nerved and awned. *Lycurus setosus* can be differentiated from the other two species in the genus by having leaf blades terminating in slender seta 0.5–10(12) mm long and acute to acuminate ligules 3–10 mm long.

Upon describing the genus with two species, Kunth (1816) suggested *Lycurus* was similar to *Phleum* L. in habit, with affinities to *Aegopogon* Humb. & Bonpl. ex Willd. Based on anatomical characteristics, Sánchez and Rúgolo de Agrasar (1986) suggested *Lycurus* be aligned with *Aegopogon* and *Tragus* Haller f. (tribe Zoyisieae). Sánchez and Rúgolo de Agrasar (1986) also pointed out the anatomical similarity between *Erioneuron* Nash (tribe Eragrostideae) and *Lycurus*. Based upon morphological similarities, Mez (1921) transferred *Muhlenbergia shaffneri* E. Fourn., considered a synonym of *Muhlenbergia depauperata* Scribn., to *Lycurus*. *Muhlenbergia depauperata* and *M. brevis* C. O. Goodd. share many morphological features with *Lycurus*, most importantly: paired spikelets, 2-nerved lower glumes with two awns, and 3-nerved lemmas (Peterson and Annable 1991). Pilger (1956) erected the subtribe *Lycurinae*, which included *Lycurus* and *Pereilema* J. Presl. Clayton and Renvoize (1986) and Valdes-Reyna and Hatch (1991) took the traditional view and place *Lycurus* in the subtribe *Sporobolinae*, along with *Calamovilfa* (A. Gray) Hack. ex Scribn. & Southw., *Crypsis* Aiton, *Muhlenbergia* Schreb., *Pereilema*, and *Sporobolus* R. Br. Based on chloroplast DNA evidence, *Lycurus* appears to be firmly embedded in the subtribe *Muhlenbergiinae*, subfamily *Chloridoideae*, along with *Bealia* Scribn., *Blepharoneuron* Nash, *Chaboissaea* E. Fourn., *Muhlenbergia*, and *Pereilema* (Duvall et al. 1994; Peterson et al. 1995, 1997).

The origin of the *Chloridoideae* (=Eragrostioideae, *sensu* Pilger 1954, 1956) appears to be in southwestern Africa, where the climate

is extremely arid, summer rainfall is common, and mean winter temperature is above 10°C (Hartley and Slater 1960). Chloridoid centers of diversity occur in southwestern Africa, northcentral (Tibesti, Sahara) Africa, and northwestern USA/northern Mexico (Clayton 1975; Hartley and Slater 1960). This wide distributional pattern suggests that the subfamily is an old one and that subsequent radiation from the African continent has occurred (Hartley and Slater 1960).

Although there is some doubt as to the specific taxon surveyed, chromosome counts for *Lycurus setosus* indicate that it is tetraploid ($2n = 40$) with a base chromosome number of $x = 10$ (Avdulov 1931; Gould 1964, 1965; J. Reeder 1967, 1971, 1977). The U.S. National Herbarium (US) has four specimens of *L. setosus* from Chihuahua and Durango, Mexico, collected by Reeder and Reeder (4877, 4884, 4890, 4898) that indicate a chromosome count of $2n = 40$.

The present study, the first analysis of soluble enzymes in *Lycurus*, was initiated to estimate the genetic diversity within and among populations of *L. setosus*. We also hoped to gain new insights into the phylogeographical history and evolutionary processes operating among populations with amphitropical disjunct distributions. Similar studies of allozyme variation in *Bealia mexicana* Scribn., *Chaboissaea atacamensis* (Parodi) P. M. Peterson and Annable, *C. decumbens* (Swallen) Reeder and C. Reeder, *C. ligulata*. E. Fourn., *C. subbiflora* (Hitchc.) Reeder and C. Reeder, *Muhlenbergia argentea* Vasey, *M. lucida* Swallen, *M. torreyi* (Kunth) Hitchc. ex Bush, and *Scleropogon brevifolius* Phil. have revealed high intraspecific variability (H ranging from 0.19 to 1.00) and high levels of genetic diversity (F ranging from 0.073 to -1.000) (Peterson and Columbus 1997; Peterson and Herrera A. 1995; Peterson and Ortiz-Diaz in preparation; Peterson et al. 1993).

METHODS

Thirteen populations representing 365 individuals were sampled from throughout the geographic range of *Lycurus setosus* (Table 1). Fresh leaf blades were collected in the field, placed in 3.6 or 5.0 ml cryotubes (NUNC), and frozen on site in liquid nitrogen.

Sample preparation and electrophoresis of enzymes followed the general methodology of Morden et al. (1987). Approximately 300 mg of mature tissue from each plant was homogenized in up to 25 drops of grinding buffer together with about 50 mg of sea sand to enhance disruption of cells. Extracts were absorbed into 2×11 mm Whatman filter paper wicks and stored at -80°C . Electrophoresis was conducted in the four gel/electrode buffer systems (L, M, N, T) as described in Morden et al. (1987). Starch concentration was mod-

TABLE 1. FIELD COLLECTIONS OF *LYCURUS SETOSUS* ANALYZED BY ENZYME ELECTROPHORESIS. Vouchers deposited at US.

ARGENTINA. **Jujuy:** Depto. Humahuaca: 20 km N of Humahuaca on Hwy 9 towards Tres Cruces, 17 Mar. 1991, *Peterson & Annable 11762*. **Mendoza:** Depto. Lujan de Cuyo, 12 km SW of Potrerillos, 26 Feb. 1991, *Peterson & Annable 11439*. **Salta:** Depto. La Poma, 4 km N of Saladillo on Hwy 40, 15 Mar. 1991, *Peterson & Annable 11746*. Depto. San Carlos, just E of Isonza and 26 km N of Amblayo, 13 Mar. 1991, *Peterson & Annable 11724*. **San Juan:** Depto. Zonda, 37 km SW of Zonda at Estancia Maradona, 29 Feb. 1991, *Peterson & Annable 11513*. **Tucuman:** Depto. Tafi del Valle, 30 km SE of Amaicha del Valle on Hwy 307, 8 Mar. 1991, *Peterson & Annable 11622*.

MEXICO. **Sonora:** Sierra El Gato, 5.7 mi E of Huachinera, 9 Oct. 1992, *Peterson & Annable 12350*.

U.S.A. **Arizona:** Coconino Co., 6 mi NW of Ash Fork on Canyon Road (39) below Antolini, 28 Sep. 1992, *Peterson & Annable 12174*. Gila Co., 3.7 mi S of Young on Hwy 288 towards Globe, 30 Sep. 1992, *Peterson & Annable 12218*. Pima Co., Santa Rita Mountains, 4.8 mi W of Hwy 83 on Forest Service 231 and 0.2 mi W on Forest Service 4053, 1 Oct. 1992, *Peterson & Annable 12246*. Yavapai Co., 8.7 mi SW of Jerome on Hwy 89A, 28 Sep. 1992, *Peterson & Annable 12184*. **New Mexico:** Grant Co., Burro Mountains, 0.3 mi N of Hwy 90 on Mill Canyon Road (Forest Service 859), 4 Oct. 1992, *Peterson & Annable 12299*. Hidalgo Co., Peloncillo Mountains, 10 mi W of Hwy 338 on Forest Service 63 in Clayton Draw, 5 Oct. 1992, *Peterson & Annable 12320*.

ified to improve gel handling and improve resolution; all gels consisted of Sigma hydrolyzed potato starch at concentrations of 10.6%, 12.0%, 11.5%, and 12.0% for the L, M, N, and T systems, respectively. For each population, samples from all individuals were included together on the same gel. Selected individuals from different populations were then analyzed together for purposes of interspecific and interpopulational comparisons.

Gels were sliced and stained for the following 14 enzymes: aspartate aminotransferase (AAT), aconitase (ACO), adenylate kinase (ADK), aminopeptidase (AMP), fructokinase (FRK), glutamate dehydrogenase (GDH), glutamate-pyruvate transaminase (GPT), isocitrate dehydrogenase (IDH), malate dehydrogenase (MDH), 6-phosphogluconate dehydrogenase (PGD), phosphoglucose isomerase (PGI), phosphoglucumutase (PGM), shikimate dehydrogenase (SAD), and triose phosphate isomerase (TPI). Banding pattern interpretations are based on known subunit structure and conserved number of loci at the diploid level. Only the faster migrating bands of IDH, assumed to be the nuclear-encoded plastid form were surveyed (Gottlieb 1982; Weeden and Wendel 1989). Loci were designated sequentially with the most anodally-migrating locus designated 1, the next 2, and so on. Alleles were designated sequentially with the most anodally-migrating allele given an *a*, the next *b*, and so on.

Values for Nei's (1972) genetic identity (*I*) and distance measures

TABLE 2. GENETIC VARIATION IN POPULATIONS OF *LYCURUS SETOSUS*: sample size (n); mean number of alleles per locus (A); mean proportion of polymorphic loci (P); 95% criterion, mean heterozygosity (H), direct count estimate; and mean fixation index (F).

| Collection No. | n | A | P | H | F |
|----------------|------|-----|------|-------|--------|
| 11439 | 29.0 | 1.4 | 42.9 | 0.429 | -1.000 |
| 11513 | 30.3 | 1.9 | 71.4 | 0.311 | -0.390 |
| 11622 | 27.0 | 1.8 | 57.1 | 0.532 | -0.833 |
| 11724 | 29.0 | 1.8 | 57.1 | 0.520 | -0.789 |
| 11746 | 30.0 | 1.7 | 64.3 | 0.569 | -0.778 |
| 11762 | 30.0 | 1.8 | 64.3 | 0.417 | -0.583 |
| 12174 | 28.0 | 1.9 | 57.1 | 0.372 | -0.527 |
| 12184 | 28.0 | 1.8 | 57.1 | 0.520 | -0.722 |
| 12218 | 27.0 | 2.1 | 78.6 | 0.450 | -0.444 |
| 12246 | 28.0 | 1.9 | 78.6 | 0.615 | -0.607 |
| 12299 | 27.9 | 1.7 | 57.1 | 0.334 | -0.413 |
| 12320 | 27.1 | 1.9 | 78.6 | 0.398 | -0.379 |
| 12350 | 23.0 | 2.0 | 71.4 | 0.385 | -0.433 |
| Total Means | 28 | 1.8 | 64 | 0.45 | -0.61 |

were computed for pairwise comparisons using BIOSYS-1 (Swofford and Selander 1989). Although all these populations are probably tetraploid in origin, an initial BIOSYS-1 run was undertaken to measure each population's genetic variability and to compute genetic identities (Nei 1972). Standard measures of genetic variation (Table 2) were computed including mean number of alleles per locus (A), proportion of polymorphic loci (P), mean heterozygosity (H), and mean fixation index (E) which measures the deviation of genotypic proportions from Hardy-Weinberg expectations (Wright 1965). The distribution of genetic variation was determined using F-statistics where F_{IS} is the fixation index within populations, F_{IT} is the overall fixation index or inbreeding coefficient, and F_{ST} measures the degree of differentiation among populations (Wright 1965, 1969; Jain and Workman 1967). The patristic distance matrix was calculated using the Prevosti distance index (Wright 1978) and after optimization of branch lengths, a corresponding phenogram (Fig. 1) using the Wagner procedure was produced (Swofford and Selander 1989).

RESULTS

Eleven enzyme systems encoded by 18 putative loci were consistently scorable by starch gel electrophoresis: AAT-1, AAT-2, ACO-1, ACO-2, AMP-1, AMP-2, GDH, GPT, IDH, PGD, PGI-1, PGI-2, PGM-1, PGM-2, SAD-1, SAD-2, TPI-1, TPI-2. Several enzymes or putative loci, viz., ADK, FRK, MDH, and PGD-2 were not scorable due to faint or inconsistent staining. Allele frequencies

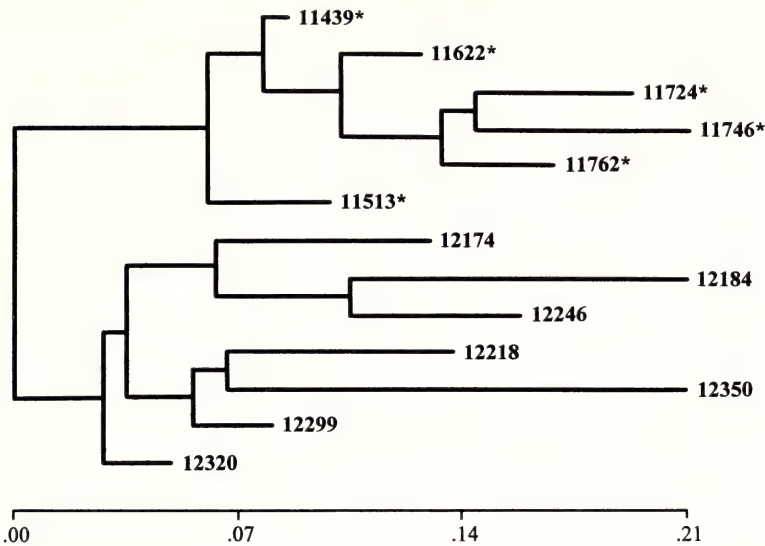


FIG. 1. Phenogram showing genetic distance among populations of *Lycurus setosus*. Correlation coefficient = 0.841; length = 0.971; numbers refer to population collections given in Table 1; populations from South America are marked with an asterisk; scale indicates distance from midpoint.

for all 13 populations surveyed appear in Appendix 1. The number of alleles per polymorphic locus ranged from two in AAT-1, AAT-2, AMP-1, AMP-2, GDH, GPT, PGD, PGM-1, PGM-2, TPI-1, and TPI-2 to six in PGI-1. The following loci were fixed for a single allele for all populations: AMP-1 and AMP-2. The largest number of alleles per locus in a population was four, occurring in PGI-1 (population 11513). There was no evidence of duplicated loci, however, AAT-1, AAT-2, GDH, and GPT were fixed for a pair of different alleles and removed from the genetic analysis.

The sample size (*n*) per population ranged from 23 to 30 individuals and the mean number of alleles per locus (*A*) within populations ranged from 1.4 to 2.1 (Table 2). The percentage of polymorphic loci (*P*) ranged from 0.429 to 0.786 and the mean heterozygosity (*H*), direct count estimate, ranged from 0.311 to 0.615, indicating a high level of heterozygosity at most polymorphic loci (Table 2). The mean fixation index (*F*) within populations, or inbreeding coefficient, ranged from -0.38 to -1.00. Genetic variability as measured in pooled populations from North and South America was: *A* = 1.7, 1.9; *P* = 60, 68; *H* = 0.46, 0.44 (Table 3).

There were 45 alleles recorded in the North American populations and 40 in the South American populations (Appendix 1, Table 3). One unique allele was detected in each of four populations 11513

TABLE 3. GENETIC VARIABILITY IN NORTH AND SOUTH AMERICAN POPULATIONS OF *LYCURUS SETOSUS*: number of populations sampled (n); mean number of alleles per locus (A); mean proportion of polymorphic loci (P); 95% criterion, mean heterozygosity (H), direct count estimate; and alleles in common and unique (u).

| Country | n | A | P | H | Alleles (u) |
|---------------|---|-----|------|-------|-------------|
| South America | 6 | 1.7 | 59.5 | 0.463 | 40 (1) |
| North America | 7 | 1.9 | 68.4 | 0.439 | 45 (6) |

(PGI-1-b), 12184 (PGI-2-c), 12320 (TPI-1-a), and 12350 (SAD-1-a). Two of these unique alleles were found in single individuals in populations 11513 and 12320; PGI-2-c (12184) was found in two individuals and SAD-1-a (12350) was found in eight individuals. In North America all seven populations shared alleles PGI-1-a & d and two populations (12174, 12350) shared allele SAD-2-a. None of these three alleles was present in South American populations. In summary, a total of six alleles are exclusively shared by North American populations and a one allele is unique in South America (Table 3).

Partitioning of genetic diversity, or the fixation of alleles at different hierarchical levels, within and among populations of *Lycurus setosus* was calculated using *F*-statistics where the fixation index within populations (F_{IS}) ranged from -0.019 to -0.927 (mean -0.723). The amount of genetic diversity among populations (F_{ST}) ranged from 0.017 to 0.456 (mean 0.256). The overall fixation index (F_{IT}) ranged from 0.008 to -0.758 (mean -0.281). The primary component of F_{IT} was F_{IS} , i.e., the F_{ST} values were much smaller, indicating greater heterogeneity within populations than among them.

A phenogram (Fig. 1) summarizes the interpopulational relationships based on genetic distance values. Six populations from South America are differentiated on a single branch at the 0.38 level or distance from root, whereas seven populations from North America are differentiated on a single branch at the 0.20 level. These two branches separating the North from the South American populations are then joined near the base at the 0.009 level.

Mean genetic identities (Nei 1972) among populations were quite variable ranging from 0.718 between population 12184 and 12350 (both from North America), to 0.978 between population 12299 and 12320 (both from North America). The mean genetic identity for all 13 populations was 0.89. A comparison of identity values among populations from North and South America indicates that the genetic variation is greater ($I = 0.89$) in North America than in South America ($I = 0.94$).

DISCUSSION

All populations of *Lycurus setosus* examined in this study show high levels of genetic variation comparable to that found in out-crossing plant species (Hamrick and Godt 1989; Hamrick et al. 1979). This is reflected in the high mean values for all populations for proportion of polymorphic loci of 0.64, heterozygosity of 0.45, and negative F values of -0.61 . All of these values indicate a consistent excess of heterozygotes (Table 2). All populations possess high levels of heterogeneity within populations (F_{IS} approaching -1 , mean of -0.723) and exhibit lower levels of genetic fixation among populations (F_{ST} mean of 0.256).

Since the phenogram (Fig. 1) was computed using genetic distance it mirrors the results inferred from genetic identities. Clearly, populations from South America form a more compact group reflecting a lower genetic variability. However, population 11513 from San Juan, Argentina, is quite variable (mean number of alleles per locus, $A = 1.9$, and proportion of polymorphic loci, $P = 71.4$) and similar to North American populations.

Genetic identities values indicated that populations from South America ($I = 0.94$) were more similar to each other than those from North America ($I = 0.89$). Both of these values fall within the range of other intraspecific identity values obtained for plant populations and are considerably higher than those reported for congeneric species (Gottlieb 1981, $I = 0.67$). Other intraspecific identity values (I) for eragrostoid grasses reported are: 0.96 for *Bealia mexicana*; 0.94 for *Chaboissaea atacamensis*; 0.82 for *C. ligulata*; 0.88 for *C. subbiflora*; 0.95 for *Muhlenbergia argentea*; 0.98 for *M. lucida*; and 0.93 for *Scleropogon brevifolius* (Peterson and Columbus 1997; Peterson and Herrera A. 1995; Peterson et al. 1993). Because there was a single unique allele present in the South American populations where less genetic variation exists and these same populations were missing six alleles found in North American populations, it seems likely that *Lycurus setosus* has recently dispersed to the Southern hemisphere.

Scleropogon brevifolius (Peterson and Columbus 1997) and *Muhlenbergia torreyi* (Kunth) Hitchc. (Peterson and Ortiz, in preparation) apparently have similar biogeographical histories. Like *Lycurus setosus*, populations of both species have lower levels of genetic variation in the Southern hemisphere and have very few or no unique alleles while lacking alleles shared by North American populations. This North to South American dispersal is seen in *Chaboissaea*, where a single species or vicariad, *C. atacamensis*, has recently dispersed from Mexico to South America from its closest sister, *C. ligulata* (Sykes et al. 1997). The north to south migration pattern is not always the case, and the reverse (south to north) is exhibited in *Bothriochloa* Kuntze

(Allred 1981) and *Erioneuron* Nash (Peterson in preparation). *Chaiboissaea*, *Lycurus*, and *Muhlenbergia*, all members of subtribe Muhlenbergiinae, have centers of diversity in North America. In contrast, *Erioneuron*, a member of the Munroinae (including *Blepharidachne* Hack., *Dasyochloa* Willd. ex Rydb., and *Munroa* Torr.) has a center of diversity in South America. Two major themes that all of these disjunctions seem to have in common is 1) recent migration, since little morphological differences and very little genetic differentiation exist, and 2) the putative dispersed species or taxon has migrated away from a center of diversity.

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APPENDIX 1. Continued.

| POPULATIONS | | | | | | | | | | | | | | |
|-------------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|--|
| | | SOUTH | | | | | | NORTH | | | | | | |
| Locus | 11439 | 11513 | 11622 | 11724 | 11746 | 11762 | 12174 | 12184 | 12218 | 12246 | 12299 | 12320 | 12350 | |
| PGM-1 | | | | | | | | | | | | | | |
| A | .000 | .032 | .000 | .000 | .000 | .033 | .018 | .500 | .241 | .071 | .000 | .000 | .022 | |
| B | 1.000 | .968 | 1.000 | 1.000 | 1.000 | .967 | .982 | .500 | .759 | .929 | 1.000 | 1.000 | .978 | |
| PGM-2 | | | | | | | | | | | | | | |
| A | .000 | .000 | .500 | .500 | .500 | .467 | .500 | .000 | .222 | .500 | .250 | .037 | .696 | |
| B | 1.000 | 1.000 | .500 | .500 | .500 | .533 | .500 | 1.000 | .778 | .500 | .750 | .963 | .304 | |
| SAD-1 | | | | | | | | | | | | | | |
| A | .000 | .000 | .000 | .000 | .000 | .000 | .000 | .000 | .000 | .000 | .000 | .000 | .174* | |
| B | .500 | .500 | .500 | .000 | .300 | .000 | .500 | .536 | .019 | .571 | .250 | .537 | .326 | |
| C | .500 | .500 | .500 | 1.000 | .700 | 1.000 | .500 | .464 | .981 | .429 | .750 | .463 | .500 | |
| SAD-2 | | | | | | | | | | | | | | |
| A | .500 | .968 | .500 | .655 | .500 | .500 | .125 | .464 | .481 | .875 | .768 | .750 | .478 | |
| B | .500 | .000 | .500 | .345 | .000 | .500 | .821 | .536 | .167 | .125 | .232 | .250 | .478 | |
| C | .000 | .000 | .000 | .000 | .000 | .000 | .054 | .000 | .000 | .000 | .000 | .000 | .022 | |
| D | .000 | .032 | .000 | .000 | .500 | .000 | .000 | .000 | .130 | .000 | .000 | .000 | .022 | |
| TPI-1 | | | | | | | | | | | | | | |
| A | .000 | .000 | .000 | .000 | .000 | .000 | .000 | .000 | .000 | .000 | .000 | .019* | .000 | |
| B | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | .981 | 1.000 | |
| TPI-2 | | | | | | | | | | | | | | |
| A | .000 | .032 | .000 | .000 | .500 | .150 | .000 | .500 | .500 | .500 | .000 | .093 | .065 | |
| B | 1.000 | .968 | 1.000 | 1.000 | .500 | .850 | 1.000 | .500 | .500 | .500 | 1.000 | .907 | .935 | |

DEMOGRAPHY OF THE ENDANGERED PLANT, *SILENE SPALDINGII* (CARYOPHYLLACEAE) IN NORTHWEST MONTANA

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ABSTRACT

I conducted a demographic study of the endangered perennial herb, *Silene spaldingii*, following >170 mapped individuals from 1987 through 1996 on a preserve in northwest Montana. *Silene spaldingii* occurs in mesic sites, but highest densities are negatively correlated with the density of the largest bunchgrass, suggesting that disturbance may play a positive role in the species' life history. Equilibrium population growth was stable over the period of the study, although significant recruitment occurred in only two of the seven years for which it could be accurately measured. *Silene spaldingii* is a long-lived perennial, with 72% of the plants observed in 1989 still present in 1994. Plants spent nearly 50% of their summers in a dormant condition, and this appears to be an important life history strategy in this semi-arid environment. Flowering, recruitment, and growth were positively correlated in time, and all were negatively correlated with summer dormancy. These demographic parameters were correlated only with mean winter temperature; however, they exhibited two-year cycles, suggesting that plants may be strongly influenced by their previous-year performance. Prescribed fire may be a useful tool for managing *S. spaldingii* at this site.

Silene spaldingii is a perennial herb endemic to the Palouse region of southeast Washington and adjacent Oregon and Idaho and is disjunct in northwest Montana (Hitchcock and Maguire 1947). Much of the habitat of *S. spaldingii* has been lost to agricultural development. Although once widespread in the Palouse region, *S. spaldingii* is now known from ca. 60 mainly isolated sites on the periphery of its former range. Most remaining populations are small and threatened by exotic weed encroachment, livestock grazing, and herbicide treatment (Gamon 1991; Lorain 1991; Schassberger 1988). *Silene spaldingii* is listed as threatened or endangered in all four states in which it occurs (Lesica and Shelly 1991).

Knowledge of demographic patterns is essential to understanding population dynamics. Estimates of vital rates, such as recruitment, growth, and mortality, obtained from demographic studies form the basis for predictions of future population growth (Menges 1990; Schemske et al. 1995). Correlations between demographic parameters and environmental variables such as climate and disturbance events can also provide insights into population dynamics and life history (Menges 1990; Schmalzel et al. 1995). Demographic studies are especially important for developing conservation management

plans for threatened species (Menges and Gordon 1996; Schmalzel et al. 1995).

The largest known population of *S. spaldingii* occurs at The Nature Conservancy's Dancing Prairie Preserve in northwest Montana. Management options such as fire are being considered for the preserve. The purpose of my study was to describe the habitat and demography of *S. spaldingii* on the preserve and to use this knowledge to help determine the long-term fate of the *S. spaldingii* population on the preserve and make recommendations regarding management.

METHODS

Species description. *Silene spaldingii* S. Watson (Caryophyllaceae) is a partially self-compatible, hermaphroditic, perennial herb, 20–40 cm tall, with a simple or branched caudex surmounting a long, slender taproot. Rhizomes or other means of vegetative propagation are lacking (Hitchcock and Maguire 1947; Lesica personal observation). Three to 20 flowers are borne in a branched terminal inflorescence. Flowers are pollinated mainly by bumblebees (Lesica 1993; Lesica and Heidel 1996), and fruit capsules mature in August. Seeds germinate with as little as four weeks of cold treatment (Lesica 1993), so germination probably occurs in fall as well as spring. Rosettes are formed the first year, after which vegetative stems are produced. Flowering usually does not occur until during or after the third season (see Results).

Study site. Dancing Prairie Preserve is ca. 300 ha in a narrow glacial valley at 825 m, 6 km north of Eureka in northwest Montana (T37N R27W S26). At Fortine, ca. 27 km south and 75 m higher, mean annual precipitation was 438 mm for 1950–1980. Mean July maximum and January minimum were 27.9° and –11.4°C respectively. *Silene spaldingii* occurs most commonly in shallow swales with deep soil dominated by large bunchgrasses (see Lesica 1993 for further details). The area had been grazed by domestic cattle, but grazing ceased when the preserve was established in 1987.

Associated vegetation. On 15–16 July 1991, after growth of dominant grass species had ceased, I established 30 113-m² (6 m radius) circular plots throughout the portion of the preserve where *S. spaldingii* occurs. I located plots so that each would contain at least ten plants of *S. spaldingii*; otherwise plot location was random. For each plot, I ocularly estimated canopy cover of all vascular plant species to the nearest 5% and recorded the size of each *S. spaldingii* plant and total density. I used principal components analysis of dominant plant cover and total plant, grass, and forb cover followed by a Pearson correlation analysis of principal components (PC) to explore

biological factors that may affect the density of *S. spaldingii* at Dancing Prairie Preserve.

Demography and life history. In mid-July 1987, four permanent monitoring transects were established in different parts of the preserve where *S. spaldingii* occurs. Transects were located subjectively to represent the population and were read annually in late July through mid-August through 1996. Each transect consisted of 40–50 adjacent 1-m² mapping quadrats placed along the transect line (Lesica 1987). The position of each *S. spaldingii* plant encountered in the quadrats was mapped and classified by growth form, reproductive status, and fecundity using the following classification:

Seedling — rosette, lacking any visible stem elongation

Dormant — no above-ground parts observed

Non-reproductive — one or more stems present but no flowers

Reproductive — one or more fertile stems present. The number of flowers was recorded for each reproductive plant.

Data analysis. *Silene spaldingii* plants may go undetected for one to several years but reappear in subsequent years (Lesica and Steele 1994). The presence of summer dormant plants can be inferred by comparing transect maps from the full sequence of years. A small proportion of these dormant plants produce small leaves that senesce and disappear by early July, while the remainder remain underground for the entire growing season (see Results). Prolonged dormancy made exact estimation of many demographic parameters difficult; however, by eliminating the initial and final two years of data, acceptable levels of error can be achieved (see Results). Plants that failed to reappear for three consecutive years were assumed dead.

Growth was defined as the proportion of plants in year t that moved to a larger size class in year $t + 1$. For analysis of growth, reproductive plants were divided into two size classes: those with <10 and those with ≥ 10 flowers. Flowering was defined as the proportion of reproductive plants. Recruitment was measured as the ratio of recruits in year $t + 1$ to reproductive plants in year t . Fecundity was measured as the number of flowers per reproductive plant. Half-life was calculated as $t \ln 2 / \ln N_x - \ln N_{x+t}$ where N_x was the number of plants at time x and N_{x+t} was the number after t years (Silvertown 1982). Pearson's correlation coefficients between mean temperature and precipitation for summer (Jul–Sep), fall (Oct–Dec), winter (Jan–Mar), and spring (Apr–Jun) and demographic parameters of the subsequent flowering season were calculated. Weather data were relativized to their overall means before analysis.

Stage-structured transition matrix projection models summarize the way in which survival, growth, and reproduction at various life-history stages interact to determine population growth (van Groe-

nendaal et al. 1988; Caswell 1989), and they can be used to summarize short-term population dynamics (Caswell 1989). There are two ways in which a reproductive plant can undergo a transition: the plant survives (Rep column) or the plant produces progeny in the rosette or vegetative classes (Rec column). The separation of these two components of reproductive transition causes an asymmetrical matrix with an extra column. The two probabilities (Rep, Rec) but must be added together in order to solve for λ . Equilibrium growth rate (λ) is the dominant eigenvalue of the transition matrix (Caswell 1989; Lefkovitch 1965). $\lambda > 1.0$ indicates population increase, while $\lambda < 1.0$ indicates decrease. λ integrates the effects of survival, growth, and fecundity of the different life-history stages into a single parameter. Details on the construction and use of matrix population models can be found in Caswell (1989) and Menges (1990).

Elasticity measures the relative change in the value of λ in response to changes in the value of a transition matrix element. Elasticity matrices allow comparison of the relative contributions of various life history transitions to population growth and fitness (de Kroon et al. 1986). Elasticities sum to unity, and regions of the matrix may be summed to compare the importance of growth and survival to recruitment (Caswell 1989).

The sporadic recruitment of rosette-class plants into the sample population precludes solving most 1-year matrices. In order to assess the population growth of the Dancing Prairie *S. spaldingii* population for 1989–1994, a “summary” matrix was constructed by summing 1-year frequency tables for the period (Caswell 1989, p. 81). This method of obtaining a multi-year estimate of population growth tends to obscure the multiplicative effects of year-to-year differences in population growth. However, a summary matrix allows multi-year assessment of elasticity.

The character of the *S. spaldingii* seed bank at Dancing Prairie is not known. Not including a seed bank in the matrix model may affect the value of λ (Kalisz and McPeck 1992), especially when it is lower than 1.0. However, it will have little effect on the analyses based on elasticities (Silvertown et al. 1993). I calculated separate elasticities for reproductive transitions and recruitment by dividing the reproductive + recruitment elasticities proportionately between the two components.

RESULTS

Associated vegetation. Vegetation supporting colonies of *Silene spaldingii* was dominated by *Festuca scabrella* (canopy cover = 70%), *F. idahoensis* (17%), and *Poa pratensis* (7%); *Antennaria microphylla* (3%), *Arnica sororia* (4%), and *Hieracium cynoglos-*

soides (3%) were common forbs. The first principal component accounted for 38% of the variance in the data and represented a gradient of increasing plant cover, especially forbs but excluding *Festuca scabrella*. The second principal component accounted for 27% of the variance and was associated with increasing cover of *F. scabrella* and decreasing cover of *Poa pratensis*. Density of *S. spaldingii* was positively correlated with PC 1 ($r = 0.43$, $P = 0.019$), and density of large (≥ 10 flowers) *S. spaldingii* plants was negatively correlated with PC 2 ($r = -0.45$, $P = 0.014$).

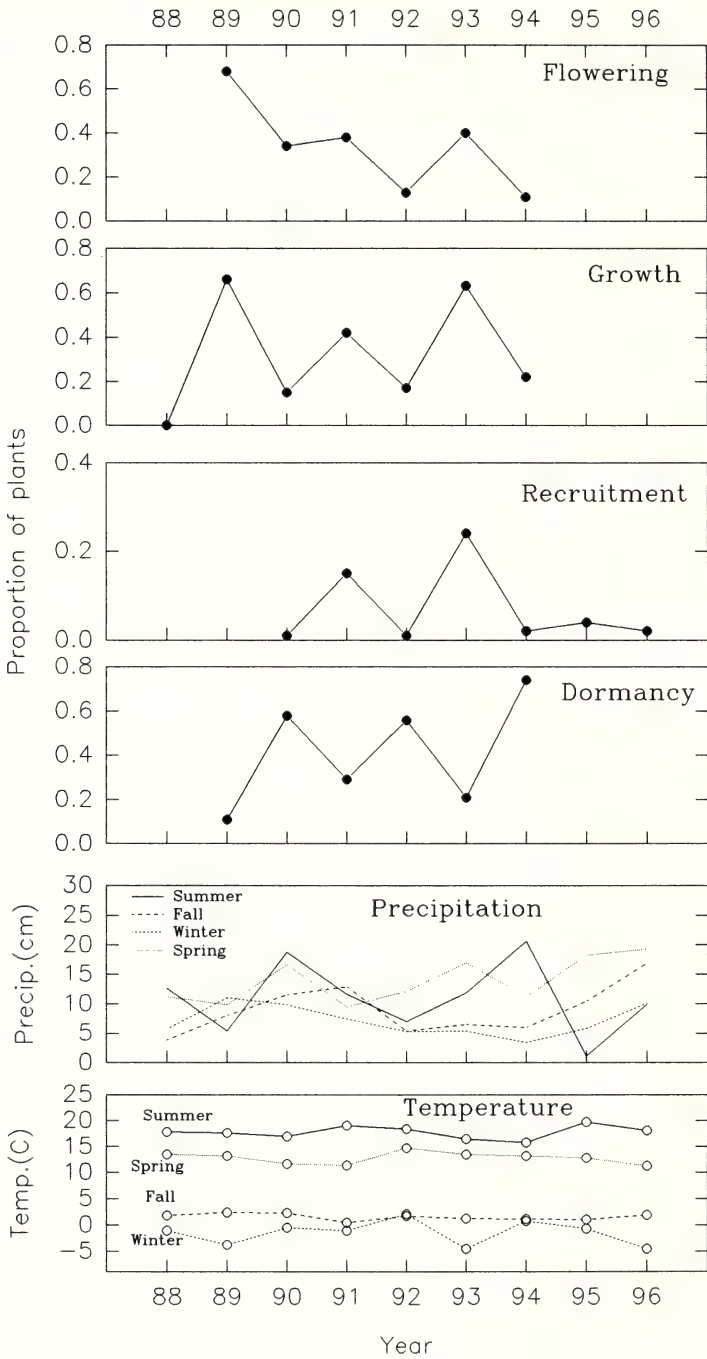
Prolonged dormancy. *Silene spaldingii* plants were not apparent above ground on 8 May 1996, but were apparent by 22 May 1995. Of the 67 plants recorded as not present in July 1995, seven (10%) were recorded in May of the same year, indicating that ca. 10% of plants assigned to the dormant size class produced short-lived, above-ground vegetation early in the growing season, while the remaining 90% did not.

A mean of 41% (SE = 10%) of *Silene spaldingii* plants exhibited summer dormancy annually from in 1989–1994, ranging from 11% in 1989 to 74% in 1994 (Fig. 1). Of the 193 episodes of prolonged dormancy recorded during this period, 75% were one year in duration, and 90% were either one or two years long. Thus, only ca. 4% ($10\% \times 41\%$) of *S. spaldingii* plants were undetected by the third year of the study (1989). The mean number of summers of dormancy for plants that persisted between 1989 and 1994 was 2.65 (SE = 0.15, $N = 72$), indicating that plants spent nearly half of their summers in dormant condition.

Growth. The percentage of plants moving into a larger size class compared to the previous year varied from 0% in 1988 to 66% in 1989 (Fig. 1).

Survivorship. The exact year that a *S. spaldingii* plant dies is difficult to ascertain because of prolonged dormancy. A plant may be dormant in year t and die in year $t + 1$, but it would appear that death occurred in year t . Fortunately, this problem does not affect the calculation of half life and has only a small effect on the shape of depletion curves.

Seventy-two percent of the plants observed in 1989 were still alive in 1994 (Fig. 2). Mortality appeared to be episodic; 22 of the 28 deaths probably occurred between the 1989 and 1990 censuses, and 15 of these occurred in adjacent quadrats of transect 4. The causes of mortality are not known. Half-life of the 1989 uneven-age cohort was 12 years, and of the 13 plants recruited in 1991, at least 9 (69%) were still alive in 1996, most mortality occurring in the first year (Fig. 2).



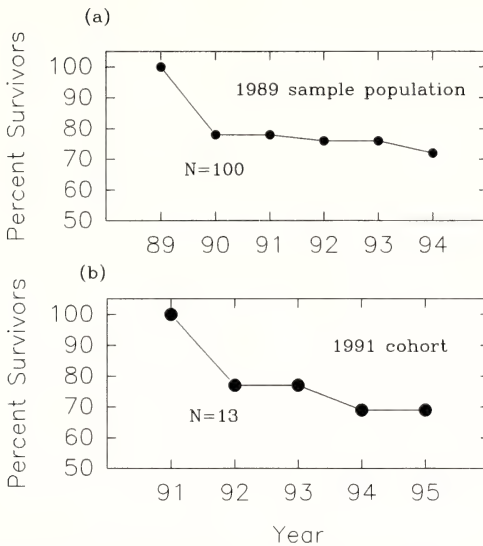


FIG. 2. (a) Depletion curve for *Silene spaldingii* sample population. (b) Survivorship curve for *S. spaldingii* cohort recruited in 1991.

Recruitment. Significant recruitment was episodic, occurring in two of the seven years in 1990–1996 (Fig. 1). Thirteen non-reproductive plants appeared in 1991, while 19 rosettes and 6 non-reproductive appeared in 1993.

Flowering. The percentage of plants flowering in 1989–1994 varied from 11% in 1994 to 68% in 1989 (Fig. 1). Twenty-six plants were recruited in 1993, and of the 17 that lived until 1996, six flowered in 1995 and an additional two flowered in 1996.

In 1987–1996, the mean number of flowers per reproductive plant was 6.11 (SE = 0.24) and varied between 3.94 in 1996 and 7.84 in 1990. The difference among years was significant (ANOVA; $F = 2.01$, $P = 0.04$, $N = 356$). Fecundity was not strongly correlated with any weather variable ($r < 0.28$). Plants with multiple flowering stems were rare throughout the study ($< 7\%$, $N = 372$).

Life history and weather correlations. Flowering, recruitment, and growth were positively correlated among years, and dormancy was negatively correlated to all three (Fig. 1, Table 1). These four demographic parameters all demonstrated a strong biennial periodicity

FIG. 1. Demographic parameters (see Methods for definitions) for *Silene spaldingii* and annual seasonal temperature and precipitation in 1988–1996.

TABLE 1. PEARSON'S COEFFICIENTS FOR CORRELATIONS BETWEEN PARAMETERS OF *SIL-
ENE SPALDINGII* DEMOGRAPHY AND CLIMATE: FLOW (PROPORTION PLANTS IN FLOWER),
DORM (PROPORTION PLANTS DORMANT), RECT (RECRUITMENT), GRTH (GROWTH), WNPR
(WINTER PRECIPITATION), SUPR (SUMMER PRECIPITATION), AND WNTM (MEAN WINTER TEM-
PERATURE). Significant coefficients (single-test $P \leq 0.05$) are in bold; parameters with-
out one coefficient >0.70 ($P = 0.12$) are not included.

| | Flow | Dorm | Rect | Grth | Wnpr | Supr |
|------|--------------|--------------|-------------|--------------|-------|-------|
| Dorm | -0.82 | — | — | — | — | — |
| Rect | 0.73 | -0.92 | — | — | — | — |
| Grth | 0.66 | -0.88 | 0.99 | — | — | — |
| Wnpr | 0.81 | -0.53 | -0.18 | 0.36 | — | — |
| Supr | -0.50 | 0.70 | -0.05 | -0.45 | -0.33 | — |
| Wntm | -0.83 | 0.85 | -0.56 | -0.78 | -0.43 | -0.21 |

that does not appear to be related to any weather variable examined, except perhaps winter temperature (Fig. 1). Mean winter temperature was strongly correlated with flowering (-), growth (-), and dormancy (+). Winter rain was correlated only with flowering (+), and summer rain was correlated only with dormancy (+) (Table 1).

Population growth and elasticity. The summary projection matrix for 1989–1994 is presented in Table 2a. Population growth rate (λ)

TABLE 2. (a) SUMMARY STAGE-BASED TRANSITION MATRIX FOR *SILENE SPALDINGII* IN 1989–1994. The Rep (reproductive) and Rec (recruitment) columns must be added together before solving for λ , the dominant eigenvalue (see Methods). Other classes are Ros (rosette), Dor (summer dormant), and Veg (non-reproductive stems). (b) MEAN ELASTICITIES FOR ABOVE STAGE TRANSITION MATRIX. The left three columns represent nonreproductive growth and survival. The reproductive column represents growth and survival of reproductives. The recruitment column represents recruitment from seed.

| | From | | | | |
|------------------|-------|-------|-------|-------|-------|
| | Ros | Dor | Veg | Rep | Rec |
| (a) | | | | | |
| To | | | | | |
| Ros | 0.045 | — | — | — | 0.097 |
| Dor | 0.727 | 0.433 | 0.398 | 0.558 | — |
| Veg | — | 0.228 | 0.219 | 0.170 | 0.112 |
| Rep | — | 0.339 | 0.281 | 0.160 | — |
| $\lambda = 1.00$ | | | | | |
| (b) | | | | | |
| To | | | | | |
| Ros | 0.001 | — | — | — | 0.020 |
| Dor | 0.020 | 0.207 | 0.095 | 0.153 | — |
| Veg | — | 0.097 | 0.047 | 0.042 | 0.027 |
| Rep | — | 0.171 | 0.071 | 0.046 | — |

was 1.00, indicating that the sample population of *S. spaldingii* was stable during this time period.

Elasticity gives the proportional importance of demographic transitions to population growth. An elasticity matrix for 1989–1994 is presented in Table 2b. There were three important transitions: (1) reproductive to dormant, (2) dormant to reproductive, and (3) dormant to dormant. These sum to greater than 50%. The sum of recruitment into the rosette and non-reproductive size classes was less than 5%.

DISCUSSION

Silene spaldingii occurs only in relatively mesic areas dominated by *Festuca scabrella* at Dancing Prairie Preserve. Within these areas, however, density and flowering of *S. spaldingii* plants are associated with lower dominance of *F. scabrella*. *Festuca scabrella* is very productive compared to *F. idahoensis* and *Poa pratensis* (Mueggler and Stewart 1980) and produces large amounts of litter annually. Litter produced by dominant plants may inhibit growth and reproduction of subordinates (Bergelson 1990; Tilman 1993), and many species require disturbances such as fire in order to persist (Hardin and White 1989; Parsons and Browne 1982). Results of the vegetation analysis support the hypothesis that *S. spaldingii* reaches its greatest abundance in sites with reduced interference from the dominant grass. Thus, disturbances such as grazing or fire may be important to the long-term persistence of this species in northwest Montana.

Silene spaldingii is a long-lived perennial. The depletion curve declines very gradually with 72% of plants surviving for at least 5 years. Furthermore, survival of first-year plants is high, indicating that most mortality occurs in early seedling stages, before July censuses. The majority of adult mortality occurred in one transect in one year. Although the cause of these deaths is not known, it appears that major causes of mortality in the sample population were environmental or catastrophic rather than demographic or genetic (Shaffer 1981). Low but temporally and spatially variable mortality also characterized *S. douglasii* populations in Oregon (Kephart and Paladino 1997).

Recruitment of *S. spaldingii* was sporadic, occurring primarily in two of the seven years for which it could be measured. Unfortunately, I was unable to detect any climatic correlates with recruitment. It is common for herbaceous perennials to exhibit irregular recruitment (Harper 1977, Chapter 19). In spite of episodic recruitment and apparently catastrophic mortality, population growth rate for *S. spaldingii* was 1.00 for 1989–1994, indicating that the sample population was stable.

Prolonged dormancy plays an important role in the life history of *S. spaldingii*. Most plants spent nearly half of their summers in dormant condition. Elasticity analysis suggests that more than 50% of population growth in this stable population was due to survival and growth of plants in the dormant stage. There was a tendency for summer dormancy to be more common when preceded by a warm, dry winter. *Silene spaldingii*'s long, deep-seated taproot undoubtedly acts as a storage organ, allowing dormancy when producing above-ground organs is not advantageous.

Flowering, growth, and recruitment were all temporally correlated, and all three of these were negatively correlated with the occurrence of prolonged dormancy. 'Favorable' years for *S. spaldingii* with high flowering, growth, and recruitment and infrequent summer dormancy occurred in 1989, 1991, and 1993. Mean winter temperature was the only weather variable strongly correlated with these demographic parameters. It is not known why cold winters should be followed by high levels of growth and flowering in *S. spaldingii*. The lack of understandable correlations with weather variables and the two-year periodicity of demographic parameters suggests that performance in one year may impact performance in the subsequent year (Sork et al. 1993). Models of mast-fruitletting suggest that members of a population with physiological constraints promoting periodic fruiting are synchronized by an extreme weather event (Silvertown 1980; Waller 1993). A similar explanation could account for the demographic patterns observed in the Dancing Prairie *S. spaldingii* population.

MANAGEMENT CONSIDERATIONS

Fire may be important for the long-term persistence of *S. spaldingii* in highly productive grasslands like those in northwest Montana. Many rare and endangered plant species require natural disturbance regimes to persist (Bowles et al. 1990; Hardin and White 1989; Parsons and Browne 1982). Fire is thought to play an important role in recruitment of *Silene regia*, a congener of eastern North American prairies (Menges 1995). Vegetation association data suggest that *S. spaldingii* could maintain larger populations where disturbance reduces litter produced by the dominant grasses. Prior to establishment of the preserve in 1987, moderate livestock grazing undoubtedly helped reduce the levels of plant litter. However, grazing by large herds of ungulates was uncommon in the bunchgrass-dominated grasslands and steppes of presettlement Intermountain Western North America (Mack and Thompson 1982), so fire was likely the predominant disturbance (Arno and Gruell 1983; Daubenmire 1970). Recruitment of *Silene spaldingii* is sporadic, perhaps depending on climate or disturbance episodes. However, it is a long-

lived perennial, enabling populations to persist many years without recruitment, so prescribed fire intervals need not be very frequent.

Results obtained from Dancing Prairie, at the extreme edge of the range of the species, cannot necessarily be extrapolated to populations remaining in the Palouse region, because demographic patterns may change with location and habitat (Kephart and Paladino 1997; Lesica and Shelly 1995). Fire should not be reintroduced at Dancing Prairie without further study. Disturbance may have adverse effects, such as exotic weed encroachment, even in fire-adapted systems (Hobbs and Huenneke 1992). Furthermore, the effect of fire on *S. spaldingii* may depend on season of burn (Howe 1994). The effects of fire on *S. spaldingii* population dynamics and on local weed populations are being investigated at Dancing Prairie Preserve.

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ERYTHRONIUM TAYLORI (LILIACEAE), A NEW SPECIES FROM THE CENTRAL SIERRA NEVADA OF CALIFORNIA

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ABSTRACT

Erythronium taylori, a new species from the central Sierra Nevada of California, is described and illustrated. This new taxon has evident affinities to other Californian *Erythronium* with unmottled leaves, especially *E. pusaterii*. The plain-leaved fawn-lilies of the Sierra Nevada have similarities in floral and other structures, suggesting that they form a single clade.

INTRODUCTION

The genus *Erythronium* consists of 25 to 30 species worldwide, of which perhaps 16 species occur in western North America. Morphological and ecological features of this western group suggest that they form a distinct lineage, well separated from the species of eastern North America and the Old World. However, relationships within this group have received little attention since the monographic work of Applegate (1935) and are not well understood.

Applegate divided the western North American species into two sections based on the presence or absence of leaf mottling. Species of sect. *Pardalinae* had mottled leaves and occurred in low-elevation habitats, and those of sect. *Concolorae* had unmottled green leaves and were most commonly found at higher elevations. In California, the latter group includes five closely related species restricted to the Cascade Mountains and Sierra Nevada, and one widespread and more distantly related species, *E. grandiflorum* (Allen 1993).

The new species of *Erythronium* described in this paper has close morphological similarities with other Sierra Nevada species of sect. *Concolorae*. It was discovered by Dean W. Taylor on 23 April 1996, along Pilot Ridge in the Tuolumne River Basin. This brings the

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number of *Erythronium* species for the Sierra Nevada to six, with three documented for Tuolumne County (Shevock et al. 1990).

Erythronium taylori Shevock & Allen sp. nov. (Fig. 1).—TYPE: USA, California, Tuolumne Co., Ascension Mountain 7.5 minute quadrangle, South Fork Tuolumne River basin, Packard Creek drainage, lower slopes of Pilot Ridge above forest road 1S13 on metamorphic rock outcrops of paleozoic marine origin, Douglas fir-mixed conifer-black oak forest, Stanislaus National Forest, T2S, R18E, sect. 4 NE $\frac{1}{4}$, 4400 ft (1340 m), 23 April 1996, *Taylor 15614* (holotype: JEPS; isotypes: CAS, K, MO, NY, RSA, US, UVIC).

Folia (18)21–28(32) cm longa 4–9 cm lata elliptica vel oblanceolata non maculata; scapus floribus singularibus vel pluribus; flores tepalis 24–40 mm longis late lanceolatis recurvis; tepala basibus aureis apicibus albis aetate subroseis, appendiculis saccatis basalibus; antheris eburneis, filamentis luteis tenuibus; stylo clavato eburneo, stigmatе integro vel brevilibato, lobi minus quam 1 mm longis.

Bulbs 4–7 cm long, 1.5–3 cm wide, often in clumps. Leaves 2, unmottled, light green without undulate margins, (18)21–28(32) cm long, 4–9 cm wide, oblanceolate to elliptic. Scapes 25–40 cm tall; flowers 1–4(8), fragrant, nodding. Perianth segments recurved to spreading, acuminate to lanceolate, 24–40 mm long, 7–12 mm wide, bicolored, terminal portion white, basal $\frac{1}{3}$ to $\frac{2}{5}$ bright yellow, fading pinkish after anthesis, inner three perianth segments with saclike folds at base. Filaments 8–12 mm, bright yellow, anthers cream-colored; style 9–11 mm, cream-white; stigma \pm entire or 3-lobed, lobes <1 mm long. Capsule narrowly obovate, 20–33 mm long on erect pedicels. Seeds ovoid, \pm 3 mm, light brown.

Paratypes. USA, California, Tuolumne Co., from type locality, 27 April 1996, *Shevock 13281* [flowering material] (CAS, FSC, JEPS, MO, RSA, UVIC); 4 May 1996, *Taylor 15631* (JEPS); 3 June 1996, *Shevock 13431* [fruiting material] (CAS, JEPS, RSA, UVIC).

Distribution, habitat and phenology. *Erythronium taylori* is currently known only from the type locality. It occurs on steep metamorphic rock outcrops in Douglas fir-mixed conifer-black oak forest, on a northeast slope below Pilot Ridge at 1340 to 1400 m, approximately 0.5 km north of the Tuolumne-Mariposa County line. This location lies at the northern end of an area of paleozoic marine sediments (Mariposa geologic sheet, 1:250,000) surrounded primarily by mesozoic granitic rocks. The southern end of this paleozoic marine area extends into the Merced River Basin toward the Chowchilla Mountains and Devil's Peak on the Sierra National Forest, Mariposa County. This new taxon appears to be locally abundant at the type locality, forming large colonies on rock terraces, ledges and

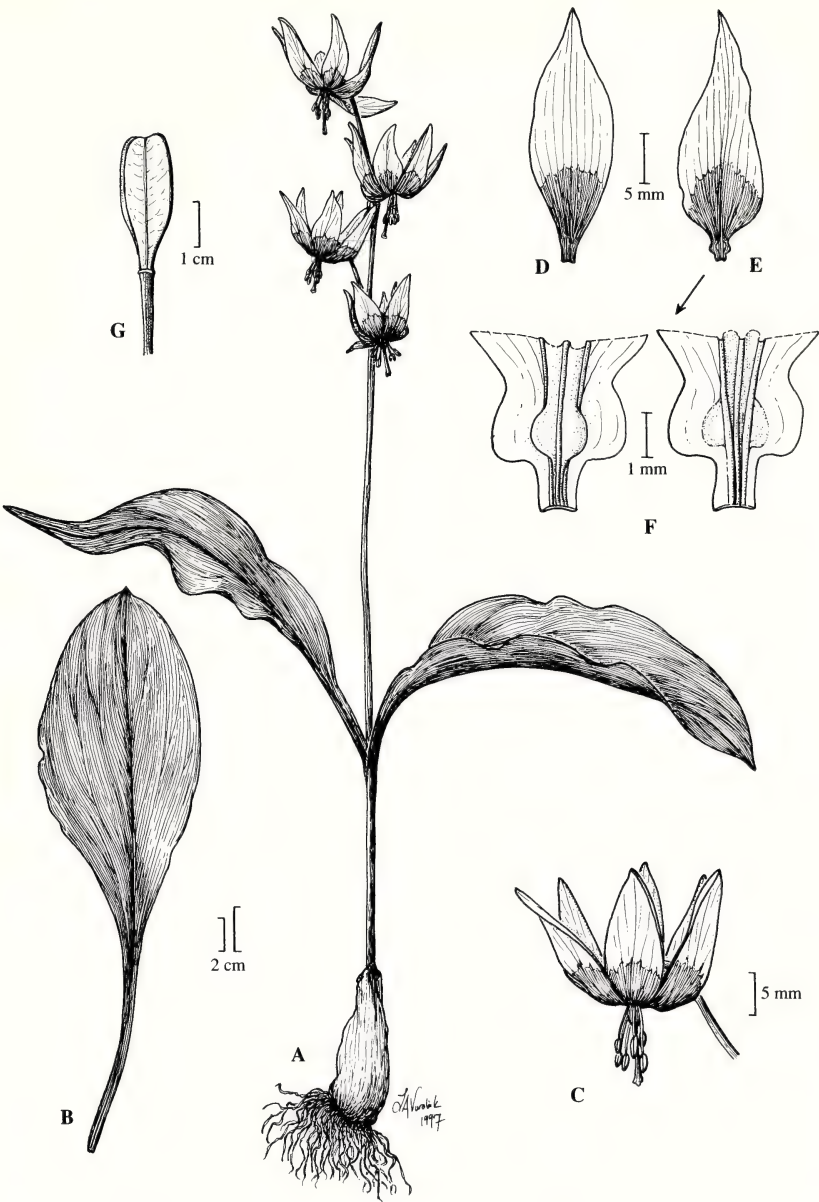


FIG. 1. *Erythronium taylori* J. R. Shevock & G. A. Allen. A. flowering scape; B. leaf; C. closeup of flower; D. outer perianth segment; E. inner perianth segment with saclike appendages; F. upper (left) and lower view (right) of saclike appendages; G. capsule.

crevices with sufficiently deep soil. The population is estimated to consist of at least a thousand plants, and additional populations should be looked for in the area.

Flowering of *E. taylori* at the type locality is from mid-April to early May. This habitat receives some snow but lacks a deep winter snowpack. Plants were observed at the bases of rock outcrops, but not in adjacent forest. This area burned in a wildfire in 1987 and some salvage logging has since occurred below the rock outcrops where the fawn-lilies are found. However, there was no evidence that *E. taylori* has been impacted adversely by the fire or adjacent timber harvesting. Associated vascular plant species include *Cheilanthes covillei*, *Cystopteris fragilis*, *Draperia stylyla*, *Dryopteris arguta*, *Dicentra formosa*, *Heuchera micrantha*, *Hieracium albiflorum*, *Penstemon newberryi*, *Polypodium hesperium*, *Polystichum imbricans*, *Spiraea densiflora*, *Streptanthus tortulosus* s.l., *Toxicodendron diversilobum*, and *Vaccinium parviflorum*. Bryophytes commonly associated with *Erythronium taylori* include *Anacolia menziesii*, *Bryum capillare*, *B. pseudotriquetrum*, *Hedwigia detonsa*, *Homalothecium pinnatifidum*, *Isopterygiopsis pulchella*, *Isothecium cardotii*, *Marsupella sphacelata*, *Orthotrichum rupestre*, *Polytrichum juniperinum*, *P. piliferum*, and *Pseudobraunia californica*.

Relationships. *Erythronium taylori* belongs to a group of five species endemic to the Sierra Nevada, which share a number of morphological features. In addition to *E. taylori*, this group includes *E. purpurascens*, a small-flowered regional endemic extending from Shasta to Tuolumne counties, and three local endemics, *E. pluriflorum*, *E. pusaterii*, and *E. tuolumnense*. *Erythronium taylori* resembles *E. purpurascens* and *E. pusaterii* in having bicolored flowers, although its flowers are generally fewer (commonly 1–3 per scape). It has in common with *E. pusaterii* and *E. tuolumnense* the presence of well defined sac-like folds at the bases of the inner perianth segments, and shares with *E. tuolumnense* a tendency (as inferred from the clumped growth habit) to produce bulb offsets. On morphological grounds, *E. taylori* appears to be most closely related to *E. pusaterii*, but further study will be needed to establish more precisely the phylogenetic relationships of these species.

REVISED KEY TO SIERRA NEVADA *ERYTHRONIUM*

- A. Leaves mottled with brown or white; stigma with well-developed lobes 1–4 mm; perianth bicolored (yellow and white); anthers cream-white *E. multiscapoideum*
- A' Leaves not mottled; stigma entire or with lobes <1 mm; perianth bicolored or yellow; anthers cream to yellow
 - B. Perianth segments bicolored, the tips white, the basal ⅓ to ½ bright yellow
 - C. Perianth segments 10–15 mm long, lacking saclike appendages at base *E. purpurascens*

- C' Perianth segments 20–45 mm long, the inner three with saclike appendages at base
 - D. Anthers yellow; filaments cream-white; leaves gen 2–5 cm wide; occurring at elevations >2000 m *E. pusaterii*
 - D' Anthers cream-white; filaments yellow; leaves gen 4–9 cm wide; occurring at elevations <1500 m *E. taylori*
- B' Perianth yellow throughout
 - E. Perianth segments 25–35 mm long, 8–12 mm wide, the inner with appendages at base; style, stigma and filaments white . . . *E. tuolumnense*
 - E' Perianth segments 15–28 mm long, 4–7 mm wide, lacking saclike appendages; style, stigma and filaments yellow *E. pluriflorum*

Rarity. *Erythronium taylori* is known only from the type locality, and is thus the rarest of the Sierran *Erythronium* taxa. Although additional occurrences may be found in further surveys, this species is probably a localized endemic. The Stanislaus National Forest will manage the habitat to conserve the species.

Like other montane *Erythronium* species in the Sierra Nevada, this species occupies a habitat with ample early-season moisture, moderate summer temperatures, and cool winters. Cultivation of *E. taylori* at lower elevations is unlikely to be successful, and because of its rarity, this species should not be collected for that purpose.

It is a pleasure to name this species for a colleague and friend who is one of California's indefatigable field workers. Dean Taylor's botanical explorations have yielded several new taxa for California (e.g., *Neviusia cliftonii* and *Carex tiogana*) and he has that special trait of sharing his knowledge and enthusiasm for the California flora with all he meets.

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A NEW BASE CHROMOSOME NUMBER AND PHYLOGENY FOR *ERIOPHYLLUM* (ASTERACEAE, HELENIEAE)

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ABSTRACT

Meiotic analysis shows that in *Eriophyllum nevinii* $2n = 19 \text{ II}$, a new base number for the genus, which now has at least six haploid numbers. The haploid numbers are explainable by either descending basic dysploidy accompanied by dysploid increase and decrease at the polyploid level, or descending basic dysploidy only.

As the dynasties of cytotaxonomy, experimental taxonomy, numerical taxonomy, and chemotaxonomy scroll away on the monitor of systematics, it may seem presumptuous to present this paper during the reign of the current regime, molecular systematics. After all, "Who counts chromosomes these days?" (Kruckeberg 1997, p. 181). But, as Constance (1964) observed, systematics is an unending synthesis. I offer the following in that spirit.

The eriophyllums are a disparate lot, radiate or discoid, from 1 cm to 2 m, in communities as different as seashore, desert, and treeline. A long list of synonyms portrays attempts to delineate taxonomic relationships. Constance (1937) used alpha taxonomic methods to prune a taxonomic thicket into 11 species and 12 varieties. Carlquist (1956) discussed generic limits of *Eriophyllum* and provided cytological and morphological information on it and *Monolopia*, *Pseudobahia*, and *Syntrichopappus*. Johnson's (1978) chemical, cytological, and morphological study of the Eriophyllinae *sensu* Rydberg (1915) included *Lembertia*, the only other genus of the subtribe. Johnson also reviewed the taxonomic history of the Eriophyllinae. Mooring and Johnson (1993) treated, respectively, the six perennial and eight annual species of *Eriophyllum*. Carlquist (1956), Johnson (1978), and Mooring (1986) reported their own and others' chromosome counts for the annual species, namely $n = 4$ (*E. lanosum*), $n = 5$ (*E. wallacei*), and $n = 7$ (*E. ambiguum*, *E. multicaule*, *E. pringlei*, *E. congdonii*, *E. nubigenum*). An $n = 8$ report for *E. pringlei*, given as a new count (Keil and Pinkava 1976), probably represents 7 II plus 2 supernumerary chromosomes. Previous reports for *E. pringlei* were 7 II , $7 \text{ II} + 1\text{B}$, and $7 \text{ II} + 2\text{B}$ (Carlquist 1956; Strother 1976; Johnson 1978). Supernumerary chromosomes are present in some of the other annuals (Strother 1972, 1976; Johnson 1978) and perennials (Mooring 1975, 1994, and unpublished). They

have been a source of error in chromosome counts for other species (Stuessy 1990).

As for the perennials, the widespread and common *E. confertiflorum* var. *confertiflorum* and *E. lanatum* are polyploid complexes in which $n = 8, 16, 24,$ and 32 (Carlquist 1956; Mooring 1975, 1994). Three other perennial taxa seem to exist only as polyploids; *E. latilobum* is tetraploid and *E. jepsonii* and *E. confertiflorum* var. *tanacetiflorum* are octoploids (Carlquist 1956; Mooring 1973). The first two are rare or uncommon (Skinner and Pavlik 1994) and probably originated independently by hybridization between *E. confertiflorum* and *E. lanatum* (Constance 1937; Munz 1959); the latter may have (Mooring 1994). Comparatively few counts have been reported for the remaining two perennials. Carlquist (1956) reported $n = 16$ in three populations of *E. staechadifolium* from Monterey and San Luis Obispo counties and in one population of *E. nevinii* from Santa Catalina Island. Mooring (1973) and Strother (in Mooring 1973), however, reported $n = 15$ in eight *E. staechadifolium* populations from Monterey to Humboldt counties, and Keil and Pinkava (1976) found $n = 15$ in a San Luis Obispo County population. The $n = 16$ counts for *E. staechadifolium* seemed to be in error. Was the $n = 16$ counts for *E. nevinii*, a taxon probably derived from *E. staechadifolium* (Constance 1937), also in error?

In this paper, I record a new chromosome number for *Eriophyllum*, discuss the range of haploid chromosome numbers in the genus, and hypothesize a phylogeny based on descending dysploidy, geographic distribution, and habitat considerations.

MATERIALS AND METHODS

Eriophyllum nevinii, rare and threatened (Skinner and Pavlik 1994), is endemic to the southern Channel Islands of California. Obtaining buds from botanical gardens was more feasible than getting them from natural populations. Unfortunately, my 1992 and 1994 collections, from the Santa Barbara Botanic Garden, turned out to be from plants of unknown provenance, believed to be members of one clone. Plants derived from cuttings whose source was known became available in 1995, at the University of California, Berkeley, Botanic Garden, and the Santa Barbara Botanic Garden, from, respectively, Middle Ranch Canyon and Mesquite Cove Canyon, San Clemente Island. Fruits from Santa Barbara Island, provided by the Santa Barbara Botanic Garden, yielded another plant. Capitula from eight plants of unknown provenance, and from five of known provenance were fixed in 1:3 acetic ethanol. Microspores were squashed in acetocarmine and examined with a phase-contrast microscope. Meiotic stages suitable for counts were uncommon. Observation of at least 10 clear diakinesis, first metaphase, or

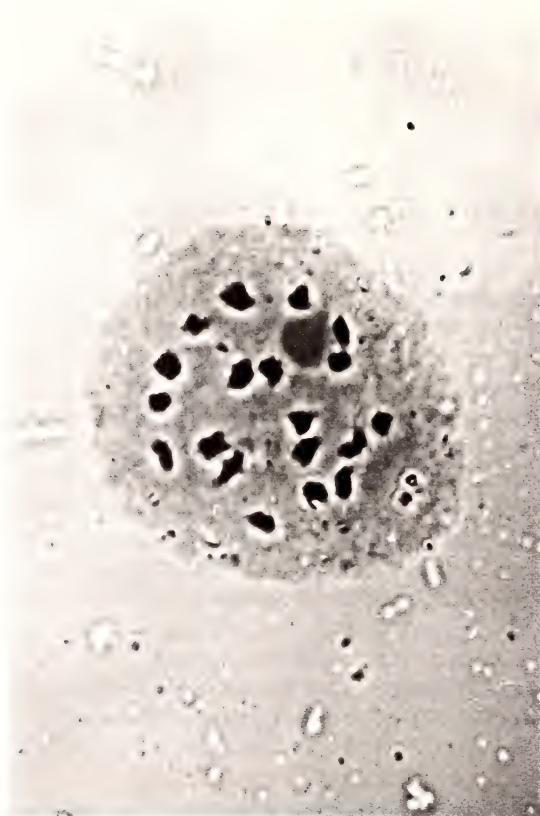


FIG. 1. Photograph of diakinesis in a microsporocyte of *Eriophyllum nevinii*, $2n = 19 \text{ II}$.

anaphase cells from each of nine plants was accompanied by sketches, camera lucida drawings, and a photomicrograph. Voucher specimens are deposited in SBBG (*Junak* 5243, 5244, 5809, 5810), JEPS (87556), and SACL (*Mooring* 3934, 3993).

RESULTS AND DISCUSSION

The microsporocytes taken in 1992 from unprovenanced plants at the Santa Barbara Botanic Garden were difficult to analyze. The chromosomes were sticky, irregularly condensed, and often overlapping. Three plants yielded counts varying from 17 to 19 II. The clearest cells suggested 18 II. Examination of the 1994 material (same site, different plants) gave 17–19 II for one plant, and 18 II + 1 I for the other. The 1995 material derived from Middle Ranch Canyon, San Clemente Island, however, showed 19 II (Fig. 1), as did 1996 material from Mesquite Cove Canyon, San Clemente Is-

land, and 1997 material from Santa Barbara Island. Reviewing the camera lucida drawings and sketches of the unprovenanced material that gave the 18 II counts suggests that what was interpreted as one bivalent was probably two greatly and irregularly condensed bivalents connected by a thread.

The distinct difference in chromosome number between *E. nevinii* and its presumed progenitor, *E. staechadifolium* (Constance 1937, p. 73), was adumbrated by Constance's (1937, p. 114) comment that *E. nevinii* is "beautifully distinct".

Possibly *E. staechadifolium* and *E. nevinii* are tetraploid derivatives with undiscovered diploid populations. If diploid populations with known base numbers do not exist, at least six haploid numbers occur in *Eriophyllum* ($n = 4, 5, 7, 8, 15, 19$). The rare annual species *E. mohavense* (Skinner and Pavlik 1994) is still uncounted.

At this point I introduce what seems to me to be a useful concept to express the amount of variation in base chromosome numbers in taxa of similar size, the "base chromosome number index", obtained by dividing the number of species per genus by the number of haploid chromosome numbers known. The base chromosome number index (hereafter BCNI) for *Eriophyllum* is $14/6$, or 2.3, i.e., one base number for every 2.3 species. No other comparable-sized genus in the Helenieae appears to have this much variation in base chromosome numbers. *Lasthenia*, with 17 species and five base numbers (Ornduff 1966), is the nearest contender, with a BCNI of $3.4 (17/5)$, one base number for every 3.4 species. Clearly, taxa with more than one base number and a sufficiently small number of species will have low BCNIs. Among the Eriophyllinae, for example, the BCNIs for *Monolopia* (3 species), *Pseudobahia* (3 species), and *Syntrichopappus* (2 species) are, respectively, 1.3, 1.0, and 1.0. The range of base chromosome numbers ($x = 4, 5, 7, 8, 15, 19$) in *Eriophyllum* suggests extensive chromosomal repatterning, a polyphyletic origin, or both. Ongoing studies by Bruce Baldwin (e.g., Baldwin and Wessa 1997) will no doubt clarify matters.

Constance (1937, pp. 72–73), before chromosome numbers were reported in *Eriophyllum*, hypothesized that the perennial *E. lanatum* ($x = 8$) most nearly represented the primitive stock of the genus. His prescient representation of phylogenetic relationships (1937, p. 73) parallels a *descending* series in the annual species: *E. nubigenum* ($n = 7$) to the other $n = 7$ species *E. congdonii*, *E. ambiguum*, *E. multicaule*, and *E. pringlei*, and to an ancestor that produced *E. wallacei* ($n = 5$) and *E. lanosum* ($n = 4$). Or, *E. multicaule* and *E. pringlei* might have been derived from the perennial and $x = 8$ *E. confertiflorum*. On the other hand, in the perennial species Constance's (1937, p. 73) *E. lanatum*–*E. staechadifolium*–*E. nevinii* phylogeny parallels an *ascending* $n = 8$ – 15 – 19 series, possibly resulting from polyploidy followed by dysploid decrease ("polyploid drop")

and increase at the polyploid level (Grant 1981, pp. 358–364, as aneuploidy rather than dysploidy).

A descending dysploidy phylogeny with *E. nevinii* rather than *E. lanatum* as the most primitive stock is also possible. Descending basic dysploidy occurs more frequently than ascending dysploidy and is known in more than 20 groups (Grant 1981). In fact, Grant (1981, p. 358) cited an 8–7–()–4–3 sequence (now 8–7–()–5–4–3) for haploid numbers in *Eriophyllum* and *Pseudobahia*, the symbol “()” representing missing numbers in the series. Haploid chromosome number, geographic distribution, habitat considerations, and, in part, crossability relationships suggest that *E. nevinii* might represent the most primitive stock, and that reduction in chromosome number has accompanied migration northward and eastward, from maritime to desert environments, and from perennial to annual habit (Tables 1, 2; Fig. 2).

Attempts to cross *E. nevinii* ($n = 19$) and *E. staechadifolium* ($n = 15$) have been unsuccessful, as have been all but one heteroploid cross in my *Eriophyllum* studies (Table 2). Attempts to cross *E. staechadifolium* and *E. confertiflorum* var. *confertiflorum* reciprocally have not yet been made, but pollinating *E. staechadifolium* with pollen from tetraploid *E. lanatum* ($n = 16$) yielded only selfs. Natural, interspecific hybrids have not been reported for these species. Clearly, no evidence exists for a hybridity connection between the maritime and mainly inland perennial species.

Eriophyllum confertiflorum var. *confertiflorum* and *E. lanatum* (both $n = 8$) bridge the chromosome number, distribution, and habitat gap between the maritime perennial species *E. nevinii* ($n = 19$) and *E. staechadifolium* ($n = 15$), on the one hand, and the annual species ($n = 7, 5$, or 4) of mostly interior plant communities on the other. Both *E. confertiflorum* var. *confertiflorum* and *E. lanatum* are polyploid complexes with a nonrandom distribution of diploid and tetraploid populations (Mooring 1975, 1994). Eighteen of the 23 *E. confertiflorum* var. *confertiflorum* populations sampled from Los Angeles County southward were diploid, suggesting that the species migrated from southwestern North America (Mooring 1994). Twenty-five of the 26 southernmost California *E. lanatum* populations are diploid (Mooring 1975 and unpublished), likewise supporting a southern origin for that taxon. The diploid populations of each complex occur in coastal communities and also in interior sagebrush and desert scrub communities (Table 1). Unfortunately, although chromosome numbers are known from about 300 populations of *E. lanatum* (Mooring 1975, 1986) and 130 of *E. confertiflorum* var. *confertiflorum* (Mooring 1994), comparatively few have been reported for four of the five annual species, *E. ambiguum* (9), *E. multicaule* (3), *E. pringlei* (9), *E. wallacei* (29), and *E. lanosum* (8) (see John-

TABLE 1. HAPLOID CHROMOSOME NUMBERS IN *ERIOPHYLLUM*. Polyploid species are not listed. Names of plant communities are taken from Munz (1959).

| Species | x | Range | Plant community |
|----------------------------|----|--|--|
| Perennials | | | |
| <i>E. nevini</i> | 19 | s. California | Coastal Sage Scrub |
| <i>E. staechadifolium</i> | 15 | s. California to Oregon | Coastal Sage Scrub, Coastal Strand, N. Coastal Scrub |
| <i>E. confertiflorum</i> | 8 | Baja California, California | Coastal Sage Scrub to Desert Scrub ecotones |
| var. <i>confertiflorum</i> | 8 | California to British Columbia, Utah, Wyoming | Northern Coastal Scrub to Sagebrush Scrub |
| <i>E. lanatum</i> | | | |
| Annuals | | | |
| <i>E. congdonii</i> | 7 | Mariposa Co., California | Foothill Woodland, Conifer Forest |
| <i>E. nubigenum</i> | 7 | Mariposa Co., California | Conifer Forest |
| <i>E. multicaule</i> | 7 | central to s. California | Coastal Sage Scrub, Chaparral, Foothill Woodland |
| <i>E. ambiguum</i> | 7 | s. California, Nevada | Foothill, Pinyon-Juniper, and Joshua-Tree Woodlands, Creosote Bush Scrub |
| <i>E. pringlei</i> | 7 | s. California, Nevada, Arizona | Chaparral, Sagebrush Scrub, Joshua-Tree Woodland, Creosote Bush Scrub |
| <i>E. mohavense</i> | ? | s. California | Creosote Bush Scrub |
| <i>E. wallacei</i> | 5 | Baja California to central California, Nevada, Utah | Chaparral, Joshua-Tree Woodland, Creosote Bush Scrub |
| <i>E. lanosum</i> | 4 | northwest Mexico, s. California, Arizona, Nevada, Utah | Creosote Bush Scrub |

TABLE 2. SUMMARY OF ARTIFICIAL HYBRIDIZATION RESULTS IN *ERIOPHYLLUM*. All are at the diploid level, unless otherwise stated. Most crosses involve one or a few plants from one population of each species.

| | |
|--|--|
| <i>E. nevinii</i> ($n = 19$) \times <i>E. staechadifolium</i> ($n = 15$) | PERENNIALS, NO HYBRIDS FORMED |
| <i>E. staechadifolium</i> ($n = 15$) \times tetraploid <i>E. lanatum</i> ($n = 16$) | |
| <i>E. lanatum</i> ($n = 8$) \times <i>E. confertiflorum</i> ($n = 8$) many combinations | PERENNIALS, VIGOROUS HYBRIDS, FERTILITY REDUCED |
| <i>E. lanatum</i> ($n = 8$) \times <i>E. ambiguum</i> ($n = 7$) | PERENNIALS \times ANNUALS, NO HYBRIDS FORMED |
| <i>E. lanatum</i> ($n = 8$) \times <i>E. congonzii</i> ($n = 7$) | PERENNIALS \times ANNUALS, STERILE HYBRIDS FORMED |
| <i>E. ambiguum</i> ($n = 7$) \times <i>E. wallacei</i> ($n = 5$) and <i>E. lanosum</i> ($n = 4$) | ANNUALS \times ANNUALS, HETEROPLOIDS, NO HYBRIDS FORMED |
| <i>E. congonzii</i> ($n = 7$) \times <i>E. wallacei</i> ($n = 5$) and <i>E. lanosum</i> ($n = 4$) | |
| <i>E. multicaule</i> ($n = 7$) \times <i>E. wallacei</i> ($n = 5$) and <i>E. lanosum</i> ($n = 4$) | |
| <i>E. nubigenum</i> ($n = 7$) \times <i>E. wallacei</i> ($n = 5$) and <i>E. lanosum</i> ($n = 4$) | |
| <i>E. pringlei</i> ($n = 7$) \times <i>E. wallacei</i> ($n = 5$) and <i>E. lanosum</i> ($n = 4$) | |
| <i>E. wallacei</i> ($n = 5$) \times <i>E. lanosum</i> ($n = 4$) | |
| <i>E. congonzii</i> ($n = 7$) \times <i>E. pringlei</i> ($n = 7$) | ANNUALS \times ANNUALS, HOMOPLOIDS, NO HYBRIDS FORMED |
| <i>E. multicaule</i> ($n = 7$) \times <i>E. nubigenum</i> ($n = 7$) | |
| <i>E. nubigenum</i> ($n = 7$) \times <i>E. pringlei</i> ($n = 7$) | |
| <i>E. ambiguum</i> ($n = 7$) \times <i>E. congonzii</i> ($n = 7$), <i>E. multicaule</i> ($n = 7$), <i>E. nubigenum</i> ($n = 7$), <i>E. pringlei</i> ($n = 7$) | ANNUALS \times ANNUALS, STERILE HYBRIDS FORMED |
| <i>E. congonzii</i> ($n = 7$) \times <i>E. multicaule</i> ($n = 7$) | |
| <i>E. multicaule</i> ($n = 7$) \times <i>E. pringlei</i> ($n = 7$) | |
| <i>E. congonzii</i> ($n = 7$) \times <i>E. nubigenum</i> ($n = 7$) | ANNUALS \times ANNUALS, VIGOROUS, FERTILE HYBRIDS FORMED |

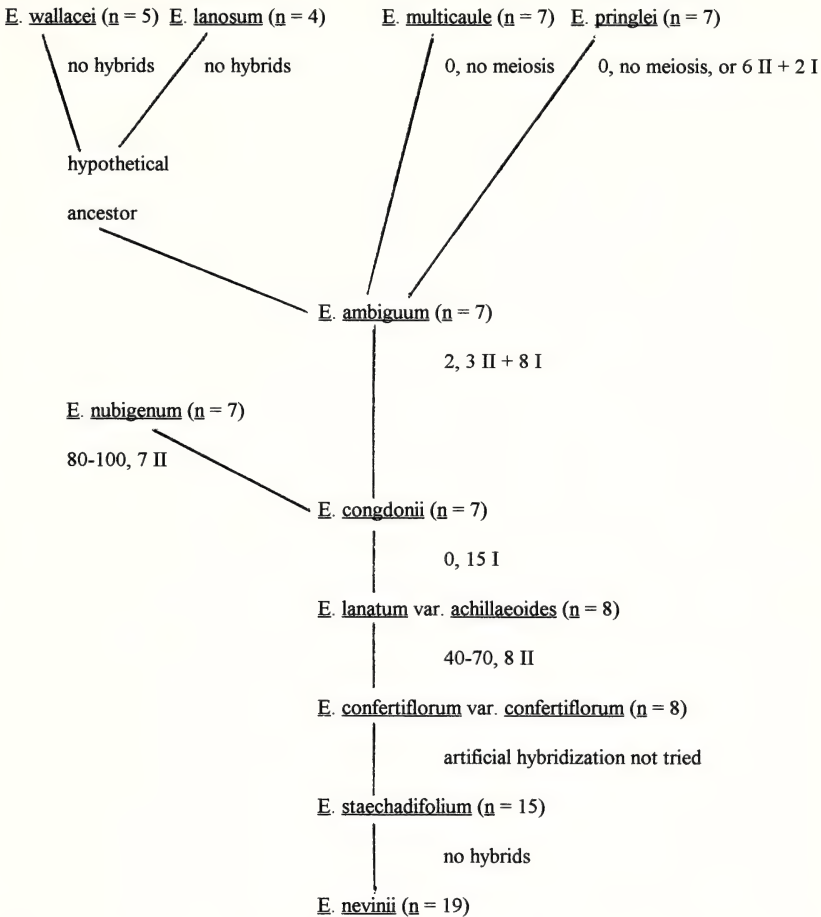


FIG. 2. Hypothetical phylogeny of *Eriophyllum*, showing percent stainable pollen and maximum meiotic configuration of artificial F_1 hybrids between the species.

son 1978). More counts would be desirable, especially from the possibly extinct *E. mohavense*.

Putative natural hybrids between *E. confertiflorum* and four varieties of *E. lanatum* have been observed (Constance 1937; Thomas 1961; Mooring 1994). At the diploid level their artificial F_1 hybrids are vigorous and almost always form 8 II at diakinesis or first metaphase, but pollen stainability averages less than 40% (Mooring 1994 and unpublished). If they did not originate from a common ancestor, morphology and geography suggest that *E. lanatum* originated from an *E. confertiflorum* var. *confertiflorum* plexus.

The annual species *E. congdonii* (n = 7) is probably nearest to *E. lanatum* (n = 8). Superficially, it closely resembles *E. lanatum*

var. *grandiflorum*. Artificial hybridizations between either *E. lanatum* var. *grandiflorum* or *E. lanatum* var. *achillaeoides* and *E. congdonii* produced vigorous F_1 hybrids with pollen stainabilities of 1% or less and meiotic configurations of 15 I (Mooring 1991). Artificial hybridization between *Eriophyllum congdonii* and the equally rare (Skinner and Pavlik 1994) *E. nubigenum* produced vigorous and fertile hybrids (Mooring 1991). On the other hand, *E. nubigenum* \times *E. lanatum* var. *grandiflorum* and *E. nubigenum* \times *E. multicaule* crosses yielded only seeds of the former (Table 2) casting doubt on Constance's (1937) hypothesis that *E. nubigenum* was a link between *E. lanatum* and *E. multicaule*.

Morphology and artificial hybridizations (Table 2, Fig. 2) suggest that *E. ambiguum* is the annual species most closely related to *E. congdonii*. They are difficult to tell apart macroscopically when grown side-by-side in the greenhouse. Hybrids constituted about 25% of one progeny, pollen stainability averaged 2%, and the maximum meiotic configuration was 3 II + 8 I (Fig. 2). *Eriophyllum ambiguum* links, in this hypothetical phylogeny (Fig. 2), the other annual species to *E. congdonii*. It forms sterile hybrids with the $n = 7$ species *E. multicaule* and *E. pringlei*, having no microspores in one cross, and forming from 2 II + 10 I to 6 II + 2 I in another (Fig. 2). Attempts to cross *E. ambiguum* with either *E. wallacei* ($n = 5$) or *E. lanosum* ($n = 4$) have been unsuccessful. Like Constance (1937), I hypothesize at least one hypothetical ancestor between these species and *E. ambiguum*, although on morphological grounds it is tempting to contemplate *E. wallacei* as more directly derived from *E. ambiguum*. Table 2 shows the results of other crosses not mentioned above.

The pattern of lower chromosome numbers in the annual eriophyllums and higher ones in the perennials fits Stebbins's (1950, pp. 167–170) discussion of chromosomal mechanisms and genetic systems. Lower chromosome numbers tend to accompany the annual habit, higher ones the perennial mode, thus helping balance fitness and evolutionary flexibility. Mode of pollination is also involved. Stebbins (1950, p. 168) observed that a "large proportion of annual species are predominantly self-pollinated." The annuals *E. nubigenum* and *E. congdonii* are partly self-compatible (Mooring 1991), and that seems to be true of the other annual species of the genus (Mooring unpublished). Contrariwise, the perennials *E. confertiflorum*, *E. jepsonii*, *E. latilobum*, and *E. lanatum* are almost completely self-incompatible (Mooring unpublished). The perennials and the $n = 7$ annual eriophyllums live in more mesic habitats than the $n = 5$ or $n = 4$ annual species (Table 1). In these environmentally more open communities, low chromosome number and partial self-compatibility would favor fitness at the expense of flexibility.

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A FIRE ECOLOGY STUDY OF A SIERRA NEVADA FOOTHILL BASALTIC MESA GRASSLAND

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ABSTRACT

In late September 1994, a lightning fire burned a portion of the annual grassland on a Sierra Nevada foothill, basaltic mesa known as McKenzie Table located approximately 28 km northeast of Fresno, California. Permanent 1-m² quadrats were established in burned and unburned plots to determine the effect of fire on the plant-species composition of McKenzie Table. Data were gathered between February and June 1995. *Vulpia microstachys* sensu lato, a native annual grass, had the highest relative density for both the unburned and the burned plots with 14.14% and 11.81%, respectively. Using percent cover as a measure of dominance, a one-way ANOVA revealed significant differences in dominance between the burned and unburned plots; *Blennosperma nanum* var. *nanum* ($P < 0.05$), *Brodiaea terrestris* ssp. *kernensis* ($P < 0.01$), *Crassula connata* ($P < 0.01$), *Lasthenia californica* ($P < 0.01$), *Montia fontana* ($P < 0.01$), *Navarretia tagetina* ($P < 0.01$), *Triphysaria eriantha* ssp. *eriantha* ($P < 0.01$), and *Trifolium variegatum* ($P < 0.01$) had significantly greater dominance values for the burned plot. *Hypochaeris glabra* ($P < 0.01$) had significantly greater dominance values for the unburned plot. The unburned plot (36 native taxa) had 12 more native taxa than the burned plot (24 native taxa), but none had significantly different dominance values. In a comparison of species composition, the burned plot had higher percentages of native species. For native species, the Shannon-Wiener index of diversity (H') is significantly greater ($P < 0.01$) for the burned plot ($H' = 5.63$) compared to the unburned plot ($H' = 3.90$). One season of results indicate that burning in the summer or fall may reduce non-native species, such as *Hypochaeris glabra*, and increase native-species diversity on McKenzie Table.

In late September 1994, a lightning fire burned 28 ha of annual grassland on top of a Sierra Nevada foothill, basaltic mesa called McKenzie Table (Fig. 1). This study was undertaken to determine if fire alters species composition and plant diversity in the annual grassland on McKenzie Table. Heady (1972) found that the composition and production of California annual grassland varies greatly during the seasons and from year to year. Seasonal changes result in fewer plants per unit area as the optimum growing climate wanes as summer progresses (Biswell and Graham 1956; Heady 1958). Yearly environmental changes may result in large shifts in grassland composition (Bentley and Talbot 1951; Heady 1961). Dominance may change yearly from grasses to forbs (Heady 1972). Fire alters the species composition within annual grasslands and the forage value for cattle (Graham 1956; Larson and Duncan 1982). The results of this study may have implications as to the use of fire to manage the annual grassland on McKenzie Table.



FIG. 1. McKenzie Table (Photo taken 1.8 km southeast of the mesa).

STUDY SITE AND METHODS

McKenzie Table is one of a series of basaltic-table mesas in eastern Fresno County, California, collectively known as Table Mountain (Fig. 2). Table Mountain is located 28 km northeast of Fresno and ranges in elevation from 518–591 m. At an elevation of 171 m, the San Joaquin River/Millerton Lake divides Table Mountain from other mesas north of the river in Madera County. The Table Mountain formation is Tertiary volcanic (basalt) formed when erosion exposed a historic San Joaquin River canyon lava flow (Division of Mines & Geology 1967). The mesa top is primarily annual grassland on shallow, moderately permeable, rocky soil of the Hideaway Series (United States Department of Agriculture 1971). McKenzie Table has numerous clumps of *Quercus douglasii* Hook. & Arn. and *Pinus sabiniana* Douglas in areas of the mesa top that have developed deeper soils. Several small vernal pools occur mostly in the northern portion of McKenzie Table. The rare *Castilleja compestris* (Benth.) Chuang & Heckard ssp. *succulenta* (Hoover) Chuang & Heckard and *Gratiola heterosepala* H. Mason & Bacigal. are known to occur in these pools (Rarefind 1995). Due to its physiography, Table Mountain tends to receive less fog during the winter than the surrounding foothills and San Joaquin Valley (personal observation from 1992 to 1995). The October 1994 to June 1995 precipitation in the central Sierra Nevada foothills was approximately 100 cm (recorded by author near Table Mountain, in the town of Auberry, at an elevation of 518 m). This was 61% above the 62 cm annual average precipitation for Auberry (United States Department of Ag-



FIG. 2. McKenzie Table is located 28 km northeast of Fresno, California, in the foothills of the Sierra Nevada Range.

riculture 1971). Cattle grazed McKenzie Table in the past, but managed grazing was discontinued on the mesa top in 1991 (Chuck Peck personal communication 1996).

In February 1995, plots were established on McKenzie Table ($37^{\circ}01'21''\text{N}$, $119^{\circ}35'59''\text{W}$; T10S R22E, S31, NW $\frac{1}{4}$), at an elevation of 550 m. Two adjacent 5041 m² study plots, one in the burned

area and the other outside the burned area, were stratified from the rest of the table grassland based on geomorphic uniformity and the spread pattern of the burn. Twenty-five 1-m² quadrats were randomly established on both plots using transect grids. Opposite corners of the quadrats were permanently established with wooden stakes. Data were collected from the 50 quadrats on 24 February, 17 March, 7 April, 28 April, 19 May, and 11 June 1995. Density (number of rooted individuals) and percent cover (dominance) were recorded, as class values ranging from 0–4, for each observed taxa within the quadrats. The density classes were as follows: 0 = 0 individuals, 1 = 1–10 individuals, 2 = 11–50 individuals, 3 = 51–100 individuals, and 4 = >100 individuals. The percent-cover classes were as follows: 0 = 0% coverage, 1 = 1–10% coverage, 2 = 11–50% coverage, 3 = 51–75% coverage, and 4 = 76–100% coverage. Cover data were also recorded for exposed rock found in a quadrat. Density and percent-cover data were converted to class medians and compared using one-way ANOVA (Sokal and Rohlf 1981). The Shannon-Wiener index of diversity (H') was calculated for both plots from native-species data (Barbour et al. 1980). H' values were calculated for all 50 quadrats to determine significance, using one-way ANOVA, between the unburned and burned plots. Only native species were used to calculate H' because non-native species could have contributed to larger H' values, thus indicating a more diverse ecosystem. The diversity of native species is relevant to management objectives that land managers use to measure the health of an ecosystem.

RESULTS

Relative density, average cover (mean \pm 1 SE), and frequency for each of the 50 taxa recorded from the study plots are presented in Table 1. Although *Crassula connata* (Ruíz Lopez & Pavón) A. Berger had similar relative density values for both plots, it was significantly dominant ($P < 0.01$) in the burned plot. *Hypochaeris glabra* L., *Vulpia bromoides* (L.) S. F. Gray, and *Erodium brachycarpum* (Godron) Thell. were the most prevalent, invasive, non-native species in the unburned plot. In the unburned plot, *Hypochaeris glabra* was significantly dominant ($P < 0.01$); in fact, it had 68% frequency in the unburned plot compared to 4% frequency in the burned plot. Plot frequencies of 100% on the burned plot were common for taxa with significantly greater dominance values. The number of recorded native taxa (36) was 12 greater on the unburned plot than the burned plot (24), but those taxa were not significantly dominant and the frequencies were generally low. Table 2 illustrates that native species relative density and percentage of recorded taxa were greater for the burned plot.

TABLE 1. RELATIVE DENSITY, AVERAGE COVER (MEAN \pm 1 SE), AND FREQUENCY OF EACH OBSERVED SPECIES ON THE UNBURNED AND BURNED PLOTS. One-way ANOVA values of average cover variation between unburned and burned plots indicated as significant (*, $P < 0.05$; **, $P < 0.01$).

| Species | Relative density | | Average cover | | Frequency | |
|--|------------------|-------------|--------------------|--------------------|---------------|-------------|
| | Unburned % | Burned % | Unburned % | Burned % | Unburned % | Burned % |
| Native | | | | | | |
| <i>Agrostis microphylla</i> Steudel. | 0.10 | 0.49 | 0.40 \pm 0.28 | 2.84 \pm 1.68 | 8 | 16 |
| <i>Amsinckia eastwoodiae</i> J. F. Macbr. | 0.05 | 0 | 1.22 \pm 1.22 | 0 | 4 | 0 |
| <i>Amsinckia menziesii</i> (Lehm.) Nelson & J. F. Macbr. var. <i>menziesii</i> | 0.05 | 0 | 0.20 \pm 0.20 | 0 | 4 | 0 |
| <i>Blennosperma nanum</i> (Hook.) S. F. Blake var. <i>nanum</i> | 0.10 | 1.56 | 0.40 \pm 0.28* | 7.28 \pm 2.11* | 8 | 64 |
| <i>Brodiaea terrestris</i> Kellogg ssp. <i>kernensis</i> (Hoover) T. Niehaus | 2.97 | 3.61 | 7.26 \pm 1.79** | 25.40 \pm 2.08** | 84 | 100 |
| <i>Castilleja attenuata</i> (A. Gray) Chuang & Heckard | 0.14 | 0 | 0.60 \pm 0.33 | 0 | 12 | 0 |
| <i>Calandrinia ciliata</i> (Ruíz Lopez & Pavón) DC. | 0.10 | 0 | 0.40 \pm 0.28 | 0 | 8 | 0 |
| <i>Chlorogalum angustifolium</i> Kellogg | 0.24 | 0.33 | 1.00 \pm 0.41 | 2.40 \pm 0.51 | 20 | 48 |
| <i>Chlorogalum pomeridianum</i> Kunth | 0 | 0.05 | 0 | 0.20 \pm 0.20 | 0 | 4 |
| <i>Clarkia purpurea</i> (Curtis) Nelson & J. F. Macbr. ssp. <i>quadrivulnera</i> (Douglas) Harlan Lewis & M. Lewis | 0.05 | 0 | 0.20 \pm 0.20 | 0 | 4 | 0 |
| <i>Crassula connata</i> (Ruíz Lopez & Pavón) A. Berger | 10.27 | 11.39 | 9.92 \pm 2.39** | 25.00 \pm 2.25** | 76 | 92 |
| <i>Deschampsia danthonioides</i> (Trin.) Munro | 2.21 | 1.40 | 4.46 \pm 1.99 | 5.86 \pm 1.91 | 28 | 56 |
| <i>Dodecatheon cleveandtii</i> E. Greene ssp. <i>patulum</i> (E. Greene) H. J. Thompson | 0 | 0.03 | 0 | 0.20 \pm 0.20 | 0 | 4 |
| <i>Eschscholzia lobbiai</i> E. Greene | 1.20 | 0 | 2.42 \pm 1.24 | 0 | 24 | 0 |
| <i>Holocarpha heermannii</i> (E. Greene) Keck | 0.27 | 0 | 1.22 \pm 1.22 | 0 | 4 | 0 |
| <i>Juncus bufonius</i> L. sensu lato | 1.21 | 1.16 | 5.48 \pm 2.25 | 6.30 \pm 2.47 | 28 | 24 |
| <i>Lasthenia californica</i> Lindley | 4.04 | 9.34 | 15.10 \pm 3.37** | 38.58 \pm 3.26** | 72 | 100 |

TABLE 1. CONTINUED.

| Species | Relative density | | Average cover | | Frequency | |
|---|------------------|-------------|-------------------|--------------------|---------------|-------------|
| | Unburned % | Burned % | Unburned % | Burned % | Unburned % | Burned % |
| <i>Layia fremontii</i> (Torrey & A. Gray) A. Gray | 0.27 | 0 | 1.22 \pm 1.22 | 0 | 4 | 0 |
| <i>Lepidium nitidum</i> Torrey & A. Gray var. <i>nitidum</i> | 9.95 | 7.86 | 15.42 \pm 2.74 | 22.96 \pm 2.47 | 84 | 92 |
| <i>Lithophragma bolanderi</i> A. Gray | 0.27 | 0 | 1.22 \pm 1.22 | 0 | 4 | 0 |
| <i>Lupinus bicolor</i> Lindley | 0.14 | 0 | 0.60 \pm 0.33 | 0 | 12 | 0 |
| <i>Minuartia californica</i> (A. Gray) Matf. | 0.05 | 0.45 | 0.20 \pm 0.20 | 2.42 \pm 1.24 | 4 | 28 |
| <i>Minuartia douglasii</i> (Torrey & A. Gray) Matf. | 0.05 | 0 | 0.20 \pm 0.20 | 0 | 4 | 0 |
| <i>Montia fontana</i> L. | 2.71 | 7.61 | 5.46 \pm 1.94** | 23.64 \pm 2.90** | 48 | 100 |
| <i>Navarretia tagetina</i> E. Greene | 1.88 | 5.79 | 3.42 \pm 1.23** | 26.70 \pm 2.56** | 48 | 100 |
| <i>Parvisedum congdonii</i> (Eastw.) R. T. Clausen | 1.80 | 0.03 | 2.64 \pm 1.68 | 0.20 \pm 0.20 | 12 | 4 |
| <i>Parvisedum pumilum</i> (Benth.) R. T. Clausen | 0 | 0.21 | 0 | 0.60 \pm 0.33 | 0 | 12 |
| <i>Phalaris arundinacea</i> L. | 0.05 | 0 | 0.20 \pm 0.20 | 0 | 4 | 0 |
| <i>Plantago erecta</i> E. Morris | 5.87 | 8.21 | 12.06 \pm 3.40 | 23.98 \pm 2.37 | 52 | 92 |
| <i>Poa secunda</i> J. S. Presl ssp. <i>secunda</i> | 0.10 | 0 | 0.40 \pm 0.28 | 0 | 8 | 0 |
| <i>Psilocarphus brevissimus</i> Nutt. var. <i>brevissimus</i> | 0.27 | 0 | 1.22 \pm 1.22 | 0 | 4 | 0 |
| <i>Selaginella hansenii</i> Hieron. | 0.05 | 0 | 0.20 \pm 0.20 | 0 | 4 | 0 |
| <i>Sidalcea calycosa</i> M. E. Jones ssp. <i>calycosa</i> | 0.29 | 0.20 | 1.20 \pm 0.43 | 1.40 \pm 0.46 | 24 | 28 |
| <i>Trifolium depauperatum</i> Desv. var. <i>amplectens</i> (Torrey & A. Gray) L. F. McDermott | 3.09 | 1.91 | 8.90 \pm 2.24 | 12.76 \pm 2.49 | 76 | 92 |
| <i>Trifolium variegatum</i> Nutt. | 2.93 | 5.59 | 6.48 \pm 2.18** | 27.72 \pm 2.40** | 48 | 100 |
| <i>Trifolium willdenovii</i> Sprengel | 2.01 | 1.70 | 7.30 \pm 2.40 | 9.54 \pm 2.69 | 56 | 48 |
| <i>Triphysaria eriantha</i> (Benth.) Chuang & Heckard ssp. <i>eriantha</i> | 1.85 | 4.90 | 4.22 \pm 1.19** | 20.92 \pm 2.61** | 64 | 92 |
| <i>Triteleia hyacinthina</i> (Lindley) E. Greene | 5.20 | 3.97 | 19.90 \pm 2.66 | 28.46 \pm 1.41 | 92 | 100 |
| <i>Vulpia microstachys</i> (Nutt.) Munro sensu lato | 14.14 | 11.81 | 22.84 \pm 3.13 | 30.86 \pm 2.47 | 92 | 96 |

TABLE I. CONTINUED.

| Species | Relative density | | Average cover | | Frequency | |
|--|------------------|-------------|--------------------|-------------------|---------------|-------------|
| | Unburned % | Burned % | Unburned % | Burned % | Unburned % | Burned % |
| Non-native | — | — | — | — | — | — |
| <i>Avena barbata</i> Link | 0.10 | 0.06 | 0.40 \pm 0.28 | 0.40 \pm 0.28 | 8 | 8 |
| <i>Bromus hordeaceus</i> L. | 3.30 | 0.44 | 8.20 \pm 3.18 | 1.62 \pm 1.23 | 36 | 12 |
| <i>Bromus diandrus</i> Roth | 0.63 | 0 | 1.82 \pm 1.24 | 0 | 16 | 0 |
| <i>Cerastium glomeratum</i> Thuill. | 0.05 | 0 | 0.20 \pm 0.20 | 0 | 4 | 0 |
| <i>Erodium brachycarpum</i> (Godron) Thell. | 10.18 | 5.34 | 22.62 \pm 2.98 | 21.32 \pm 2.49 | 100 | 100 |
| <i>Gnaphalium luteo-album</i> L. | 0.05 | 0 | 0.20 \pm 0.20 | 0 | 4 | 0 |
| <i>Hordeum murinum</i> L. ssp. <i>leporinum</i> (Link) Arcang. | 0.36 | 0 | 1.62 \pm 1.23 | 0 | 12 | 0 |
| <i>Hypochoeris glabra</i> L. | 2.95 | 0.03 | 10.54 \pm 2.57** | 0.20 \pm 0.20** | 68 | 4 |
| <i>Sonchus asper</i> (L.) Hill ssp. <i>asper</i> | 0.05 | 0 | 0.20 \pm 0.20 | 0 | 4 | 0 |
| <i>Vulpia bromoides</i> (L.) S. F. Gray | 5.40 | 4.40 | 12.38 \pm 2.80 | 13.58 \pm 2.60 | 64 | 88 |
| <i>Vulpia myuros</i> (L.) C. Gmelin sensu lato | 0.85 | 0 | 2.84 \pm 1.68 | 0 | 16 | 0 |
| Exposed Rock | — | — | 27.44 \pm 1.69 | 31.80 \pm 1.30 | 100 | 100 |
| Total | 99.89 | 99.87 | — | — | — | — |

TABLE 2. A DENSITY AND SPECIES PERCENT COMPOSITION COMPARISON OF NON-NATIVE TO NATIVE TAXA IN UNBURNED AND BURNED STUDY PLOTS.

| Species Type | Unburned plot | | Burned plot | |
|--------------------|--------------------|----------------------------------|--------------------|----------------------------------|
| | Relative density % | Species composition % of 47 taxa | Relative density % | Species composition % of 29 taxa |
| Native Species | 76 | 77 | 90 | 83 |
| Non-native Species | 24 | 23 | 10 | 17 |

The diversity results are as follows:

Shannon-Wiener Diversity Index (H')

Unburned plot 3.90

Burned plot 5.63*

* significantly greater ($P < 0.001$)

The scale ranges from 0 (only 1 species) to 7 (very diverse ecosystem) or greater (Barbour et al. 1980).

Although *Agrostis microphylla* Steudel dominance was not significantly different between the unburned and burned plots, it was an important find since it was previously unknown from the Sierra Nevada (York 104A [JEPS]). Harvey (1993) describes the range of *Agrostis microphylla* in California as the southern North Coast Ranges and North, Central, and South Coast subregions.

DISCUSSION

The results of this study indicate that fire can significantly alter species composition and diversity in annual grasslands. Eight native annuals and a perennial, *Brodiaea terrestris* Kellogg ssp. *kernensis* (Hoover) T. Niehaus, had significant responses to the fire. The increased presence of *Blennosperma nanum* (Hook.) S. F. Blake var. *nanum*, *Lasthenia californica* Lindley, *Navarretia tagetina* E. Greene, and *Triphysaria eriantha* (Benth.) Chuang & Heckard ssp. *eriantha* during the growing season following the fire suggests that these species have seed that responds positively to fire scarification and/or the removal of the thatch coupled with the additional nutrients released by the fire stimulated germination and increased seedling survival. Fire removes the thatch barrier while providing a source of nutrient-rich ash which leads to enhanced growth of herbaceous plants (Barbour et al. 1993). The removal of thatch has more of an effect on diminutive species, such as *Crassula connata* and *Montia fontana* L., since these plants appear to require early contact with mineral soil to germinate and grow before conditions become intolerable due to competition and soil desiccation.

The significant increase in dominance of *Brodiaea terrestris* ssp. *kernensis* in the burned plot cannot be explained by an increased seed germination and survival rate. It takes more than one growing season for cormous plants, such as *Brodiaea terrestris* ssp. *kernensis*, to develop from seed to a reproductive adult. Since brodiaeas, like many geophytes, may remain dormant or only produce leaves and forego flowering as a response to environmental conditions (personal observation), there may have been just as many *Brodiaea terrestris* ssp. *kernensis* corms in both plots. The nutrient flush from the ash may have stimulated *Brodiaea terrestris* ssp. *kernensis* to flower in the burned plot.

Fire significantly reduced the non-native *Hypochaeris glabra* from the study area. *Hypochaeris glabra* is a prolific producer of small, far-ranging cypselsae (personal observation). These diminutive cypselsae become lodged in the organic layer making them more susceptible to fire. In comparison, *Erodium brachycarpum* was not affected by the fire. Larson and Duncan (1982) found that an annual-grassland fire, on the nearby San Joaquin Experimental Range in Madera County, had no effect on *Erodium botrys* (Cav.) Bertol. The seeds of *Erodium* spp. have a self-burial mechanism allowing the seeds to escape being damaged by fire (Young et al. 1975).

Having a significantly greater plant diversity one season after a burn is consistent with the results of a burn study in southern California chaparral (Keeley et al. 1981). The significant increase in diversity and in dominance of eight native annual plants, combined with the significant decrease in dominance of non-native *Hypochaeris glabra*, are all indications that fire maybe a useful tool to restore and maintain biodiversity on McKenzie Table. It is possible that the virtual extirpation of *Hypochaeris glabra* from the burned plot may have contributed to the increased plant diversity. Schierenbeck (1995) noted the potential impacts from non-native species as being a decreased biodiversity, changes to successional patterns, genetic contamination, and physical as well as functional changes to ecosystems. Future research should focus on the continued collection of data from my study plots to learn the effects of fire over the long-term and with varied frequency, and the effectiveness of other management methods, such as cattle, to maintain biodiversity.

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A SYSTEMATIC STUDY OF THE *MIMULUS WIENSII* COMPLEX (SCROPHULARIACEAE: *MIMULUS* SECTION *SIMIOLUS*), INCLUDING *M. YECORENSIS* AND *M. MINUTIFLORUS*, NEW SPECIES FROM WESTERN MEXICO

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ABSTRACT

I grew cultures of 14 diverse populations representative of the *Mimulus wiensii* complex of the Sierra Madre of western Mexico and compared them morphologically, cytologically, and as to their ability to hybridize one with another and with a set of six reference populations to which they might be related. The morphological comparisons indicated that *M. wiensii* Vickery was more polymorphic and widespread than previously thought. In addition, the comparisons revealed two morphologically clearly distinct, new species. The cytological studies showed *M. wiensii* to be diploid with $n = 16$ chromosomes, and the new species to be polyploid with $n = 32$ chromosomes for the first species and $n = 32, 32\pm, 48\pm$, and $64\pm$ chromosomes for the second. The experimental hybridizations demonstrated that the various populations of *M. wiensii* cross readily with each other but do not cross with the other reference populations or with either of the new species. The two new species do not cross with each other or with any of the reference populations. The first new species is named *M. yecorensis* sp. nov. for its region of occurrence and the second, *M. minutiflorus* sp. nov. for its most prominent characteristic.

RESUMEN

Poblaciones del complejo *Mimulus wiensii* fueron comparadas con respecto a sus características morfológicas, citológicas, y a sus capacidades de formar híbridos. Las poblaciones de la especie *M. wiensii* se encontraron tener $n = 16$ cromosomas y formar híbridos fértiles entre ellos pero no con las otras poblaciones referencia o con *M. yecorensis* y *M. minutiflorus*. Las poblaciones de *M. wiensii* son fenotípicamente más variables y tienen un rango más extenso que originalmente supuesto. *Mimulus yecorensis* sp. nov. se encontró entapetes densos y bajos. Ella posee $n = 32$ cromosomas y casi nunca formó híbridos con otras poblaciones del complejo. *Mimulus minutiflorus* sp. nov. tiene tallos erguidos, delicados, y tiesos con flores muy pequeñas. Ella posee $n = 32, 32\pm, 48\pm, 64\pm$ cromosomas y formó solo un híbrido quando cruzado con otras poblaciones del complejo.

The opening of the Durango-Mazatlan portion of México 40 highway nearly 40 years ago greatly facilitated the botanical exploration of the central Sierra Madre Occidental. The first new *Mimulus* species to come to light was *M. wiensii* Vickery, collected by Delbert Wiens in 1959 (Vickery 1973). Since then, additional collections of *M. wiensii* and distinctive forms apparently related to it have been collected in the Sierra Madre along Route 40 as well as to the north and south of it. The most distinctive populations do not appear to

match any described species (Grant 1924; Gentry 1947; Kearney and Peebles 1951; Munz 1959; Shreve and Wiggins 1964; Wiggins 1980; Thompson 1993) or any specimens in the herbaria of the University of California-Berkeley (UC, JEPS), Stanford (DS), Harvard (GH), the U.S. National (US), University of Michigan (MICH), and Tucuman (LIL).

In order to elucidate their specific status, these distinctive new populations were compared morphologically, cytologically, and as to their ability to cross with each other, with other members of the *M. wiensii* complex, and with other known *Mimulus* species of the area.

MATERIALS AND METHODS

A living collection of 14 cultures of populations of the *M. wiensii* complex plus 6 reference cultures of populations of species to which they might be related was assembled for study in a greenhouse at University of Utah. The populations of the complex came from as far south as Hidalgo and as far north as Arizona, but they came mainly from the central Sierra Madre of western México (Table 1). The study populations provide a good sample of the *M. wiensii* complex with one possible exception, *M. pennellii* H. S. Gentry. My examination of the type specimen of *M. pennellii* suggests to me on morphological grounds that that species is part of the complex. However, unfortunately, it was not obtainable for this experimental study because it grows in the mountains of Sinaloa, which are dangerous due to drug traffic.

The reference cultures included two of *M. wiensii* Vickery, the most abundant species of the complex, two of *M. dentilobus* Rob & Fern, belonging to a related complex occurring to the north, and two of *M. glabratus*—one of diploid *M. glabratus* var. *fremontii* (Benth.) Grant and one of tetraploid *M. glabratus* H.B.K. var. *glabratus*—of the related *M. glabratus* complex which is widespread throughout western Mexico. *Mimulus glabratus* var. *fremontii* includes *M. madrensis* Seem, (based on my study of the type of *M. madrensis*), thus disposing of the only other published species that was potentially part of the *M. wiensii* complex.

Seeds of the study populations were collected by me and my collaborators over a period of years (Table 1). The seeds were sown and the plants propagated in a greenhouse at University of Utah.

The morphological characteristics of the plants of the study populations and of the reference populations were observed and compared as the plants developed, flowered, and set seed.

Chromosome counts for the 14 populations of the *M. wiensii* complex used in this study were made from various stages of microsporeogenesis using standard aceto-carmine squash methods as previ-

TABLE 1. ORIGINS AND CHROMOSOME COUNTS OF THE STUDY POPULATIONS OF THE *MIMULUS WIENSII* COMPLEX (*MIMULUS*, SECTION *SIOLUS*). All populations were grown under my culture numbers. Vouchers are in the Garrett Herbarium of the University of Utah (UT). An asterisk indicates populations used in the experimental hybridizations.

New Collections of the *M. wiensii* complex:

Mimulus wiensii Vickery. *n* = 16—MÉXICO: Hidalgo, El Chico National Park north of Pachuca, culture 13094* (*P. Bretting*, *s.n.*, 11 Oct. 1979); Chihuahua, Barranca del Cobre, culture 13095* (*R. A. Bye* 9725, 31 May 1980); Créel, culture 13008* (*R. A. Bye* and *W. A. Weber* 8391, 19 Oct. 1977); La Cascada near Créel, culture 12197* (*R. K. Vickery, Jr.* 2880, 3 May 1976); Durango, 11 km nw of Santiago Papasquero, culture 13460 (*R. Díaz* 72 and *R. D. Worthington* 9614, 9 Jan. 1983); route 40 w of La Ciudad, culture 13485 (*S. Sutherland*, *s.n.*, 11 June 1984); Lecheria, culture 12206* (*R. K. Vickery, Jr.* 2889, 9 May 1976); km 177 on route 40, culture 12220* (*R. K. Vickery, Jr.* 2903, 12 May 1976); crest of Sierra Madre, route 40, culture 12222* (*R. K. Vickery, Jr.* 2905, 12 May 1976).

Mimulus dentilobus Rob. & Fernald. *n* = 16—USA.: AZ, Greenlee, CO, Eagle Creek, culture 13004 (*W. L. Minckley & Assoc.* 29-VI-77).

Mimulus yecorensis n. sp. *n* = 32—MÉXICO: Sonora, Yecora, culture 13257* (*D. A. Polhemus*, *s.n.*, April 24, 1982);

Mimulus minutiflorus n. sp. *n* = 32—MÉXICO: Durango, crest of the Sierra Madre, culture 12218* (*R. K. Vickery, Jr.* 2901, 12 May 1976); Morelos, Tepozteco Temple, culture 13518 (*S. Sutherland* *s.n.*, 8 April 1985); *n* = 32 ±, 48 ±, 64 ±—MÉXICO, Durango, El Palmito, culture 7169* (collected with *Breedlove* 7231, March 1965, which is *M. glabratus* H.B.K. var. *glabratus*).

Reference Populations used in this study.

Mimulus dentilobus Rob. & Fernald. *n* = 16 (*Mukherjee* et al. 1957, *Vickery* et al. 1978)—MÉXICO: Sierra Charro, Chihuahua, 5324* (*H. S. Gentry* 8073, April 1948);—USA: AZ, Eagle Creek 13007* (*L. A. McGill* 1415, 7 June 1977).

Mimulus wiensii Vickery. *n* = 16 (*Mia* et al. 1964)—MÉXICO: Durango, crest of Sierra Madre, Highway 40, culture 6272* (Note culture number 6272 = culture 6212). West of the crest of the Sierra Madre, Highway 40, ca. 1 km west of the previous population, culture number 6273* (*R. K. Vickery, Jr.* 2616, 16 June 1960).

Mimulus glabratus var. *fremontii* (Benth.) Grant. *n* = 15 (*Vickery* et al. 1985)—

MÉXICO: Durango, Durango, culture 12215* (*R. K. Vickery, Jr.* 2898, 11 May 1976).

Mimulus glabratus H.B.K. var. *glabratus*. *n* = 31 (*Mia* et al. 1964)—MÉXICO, Durango, El Salto, culture 6209* (*D. Wiens* 2635, 23 August 1959).

ously described (*Vickery* et al. 1985). Twenty or more cells were studied from 1–4 plants of each population except for cytogenetically difficult population 7169, for which 134 cells were studied from 10 plants (Table 2). For each population representative cells were recorded with sketches or camera lucida drawings. The chromosome counts for the 6 reference populations had already been ascertained (Table 1).

For the experimental hybridization study, 16 populations—10 of the study populations and all 6 of the reference populations—were crossed in as many combinations as possible (Table 3). For each cross the pistils of 10 or more flowers of the female parent were

TABLE 2. CHROMOSOME NUMBERS AND THEIR FREQUENCIES FOUND FOR CULTURE 7169 OF THE POPULATION OF *MIMULUS MINUTIFLORS* SP. NOV. FROM EL PALMITO, DURANGO, MÉXICO (GANESAN 1990). Arrows and bold face type indicate ploidy levels and frequencies with which they were observed.

| $n =$ | Number of cells |
|-------------|-----------------|
| 29 | 3 |
| → 32 | 23 |
| 33 | 10 |
| 34 | 5 |
| 35 | 8 |
| 36 | 8 |
| 37 | 2 |
| 38 | 1 |
| 45 | 3 |
| 46 | 4 |
| 47 | 4 |
| → 48 | 23 |
| 49 | 4 |
| 52 | 1 |
| 60 | 1 |
| 61 | 3 |
| 62 | 4 |
| 63 | 2 |
| → 64 | 20 |
| 65 | 3 |
| 66 | 2 |
| | <hr/> 134 |

hand pollinated with pollen from the male parent. The flowers were not emasculated for two reasons. First, the presence of some seeds resulting from self-pollinations led to better, more vigorous growth of the ovary thus improving the chances of hybrid seeds developing. Second, when the seeds were harvested, sown and the seedlings grown, seedlings resulting from self-pollinations provided clear examples of the female parent for direct comparison with the putative F_1 hybrids, thus facilitating their recognition. A seedling was considered to be a hybrid if it exhibited trait(s) of the male parent not present in the female parent, e.g., anthocyanin leaf markings. For each cross 10, if there were that many, F_1 hybrids were grown to maturity. Those that flowered were self-pollinated, and the resulting seeds collected, counted, and the mean seed set calculated (Table 3). An average of 54 capsules was collected and counted for each cross.

RESULTS AND DISCUSSION

Morphological comparisons revealed that the study populations included 1 population of *M. dentilobus*, 9 of *M. wiensii*, and 4 that

TABLE 3. F₁ HYBRID RESULTS FOR TEST CROSSES OF 10 SELECTED NEW COLLECTIONS OF *MIMULUS* FROM WESTERN MEXICO WITH EACH OTHER AND WITH THE 6 REFERENCE POPULATIONS (AND EACH OTHER)—THEIR APPARENT CLOSEST RELATIVES AND GEOGRAPHIC NEIGHBORS. Numerical data are means of seed sets of F₁ hybrids. Note: "h" indicates non-flowering F₁ hybrid; "f" indicates combination failed; "—" means combination not tried.

| | 5324 | 13007 | 12215 | 6209 | 6272 | 6273 | 12206 | 12220 | 12222 | 13008 | 13094 | 13095 | 12197 | 13257 | 12218 | 7169 |
|---|------|-------|-------|------|------|------|-------|-------|-------|-------|-------|-------|-------|-------|-------|------|
| Reference Populations | | | | | | | | | | | | | | | | |
| <i>M. dentilobus</i> | | | | | | | | | | | | | | | | |
| 5324 n = 16 | 7.8 | 0.6 | f | — | 0.0 | — | f | — | f | — | — | — | 1.9 | f | 0.0 | — |
| 13007 n = 16 | 7.6 | 25.5 | f | — | f | f | f | f | 0.0 | f | f | — | f | — | 0.0 | f |
| <i>M. glabratus</i> v. <i>fremontii</i> | | | | | | | | | | | | | | | | |
| 12215 n = 15 | f | f | 18.9 | — | f | f | f | f | f | f | f | f | f | f | 0.0 | f |
| <i>M. glabratus</i> v. <i>glabratus</i> | | | | | | | | | | | | | | | | |
| 6209 n = 31 | — | — | — | 19.9 | — | f | — | — | f | f | f | — | — | — | — | f |
| <i>M. wiensii</i> | | | | | | | | | | | | | | | | |
| 6272 n = 16 | f | f | f | f | 3.9 | 17.8 | 13.0 | 0.6 | 0.0 | 0.0 | 32.0 | h | 11.9 | h | 0.0 | f |
| 6273 n = 16 | — | f | f | — | 0.0 | 3.8 | — | h | — | 0.0 | 0.0 | h | h | — | f | f |
| New Collections: | | | | | | | | | | | | | | | | |
| <i>M. wiensii</i> | | | | | | | | | | | | | | | | |
| 12206 n = 16 | h | f | f | — | 64.8 | — | 26.0 | — | 7.9 | — | — | — | 4.5 | f | f | — |
| 12220 n = 16 | — | f | f | — | 0.0 | 5.5 | — | 5.2 | — | 0.0 | 3.2 | 6.9 | 2.9 | f | f | — |
| 12222 n = 16 | f | f | f | — | 72.5 | — | 33.2 | — | 27.8 | — | — | — | 11.8 | f | f | — |
| 13008 n = 16 | — | f | f | f | 18.1 | 5.6 | h | 3.0 | — | 22.5 | 4.5 | 20.2 | 1.1 | f | f | f |
| 13094 n = 16 | — | f | f | f | h | h | — | h | — | 13.7 | 43.6 | 4.6 | 11.9 | f | f | f |
| 13095 n = 16 | — | f | f | f | 28.7 | 13.6 | — | 8.7 | — | 76.5 | 32.6 | 73.2 | 31.6 | f | f | f |
| 12197 n = 16 | f | f | f | — | 7.4 | 5.5 | f | f | 11.7 | 3.2 | 16.5 | 14.0 | 34.0 | f | f | f |
| <i>M. yecorensis</i> | | | | | | | | | | | | | | | | |
| 13257 n = 32 | f | — | f | — | f | — | f | f | f | h | f | f | f | 16.0 | f | f |
| <i>M. minutiflorus</i> | | | | | | | | | | | | | | | | |
| 12218 n = 32 | f | f | 0.0 | — | f | f | f | f | f | f | f | f | f | f | 57.4 | 4.6 |
| 7169 n = 32±, 48±, 64± | — | f | f | f | f | f | — | f | — | f | f | f | 1.3 | f | 8.2 | 74.0 |

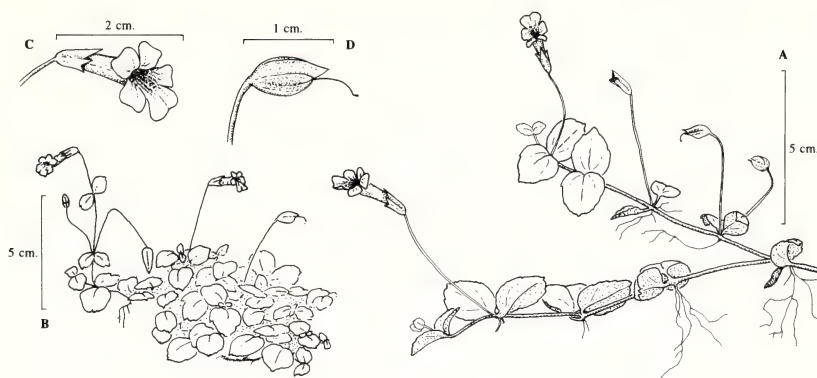


FIG. 1. *Mimulus yecorensis* sp. nov. A. a branch drawn from a live plant grown from seeds of the type collection UT 119,044 B. habit, whole plant. C. flower. D. fruiting calyx.

appeared to be distinctive enough to represent 2 new species (Table 1). One of the latter populations, 13257, from near Yecora, Mexico, differed markedly from the rest of the complex in its growth habit. The plants formed dense, low-growing mats with delicate flowers rising above the mats on long (2.5–4 cm), slender pedicels (Fig. 1). The other 3 distinctive populations (7169, 12218, and 13518) formed a morphologically similar group that differed from the rest of the complex in having very small flowers (5–6 mm long versus 10–12 mm or more). Also, the plants had erect, delicate, wiry stems (Fig. 2), in contrast to the more succulent, stems of *M. wiensii* and the population from near Yecora.

The cytological studies revealed that all the *M. wiensii* populations were diploid with $n = 16$ chromosomes as was the population of *M. dentilobus* (Table 1). In contrast, the new species were polyploid. The Yecora population had $n = 32$ chromosomes. Of the very small flowered populations two (12218 and 13518) had $n = 32$ chromosomes, whereas the third (7169) had $n = 32 \pm$, $n = 48 \pm$, and $n = 64 \pm$ chromosomes (Table 2). Population 7169 was so cytologically variable as to suggest much aneuploidy and probably back crossing, as well, among its plants.

The crossing experiments revealed only tenuous relationships among the *M. wiensii*, *M. dentilobus*, and *M. glabratus* complexes (Table 3). Within the *M. wiensii* complex, the various populations of *M. wiensii* hybridized readily—only 2 failures among the 53 combinations tested (Table 3).

The Yecora population (13257) formed only non-flowering F_1 hybrids with two of the *M. wiensii* populations. The inability of population 13257 to exchange genes with members of the complex coupled with its striking morphological distinctiveness and tetraploid

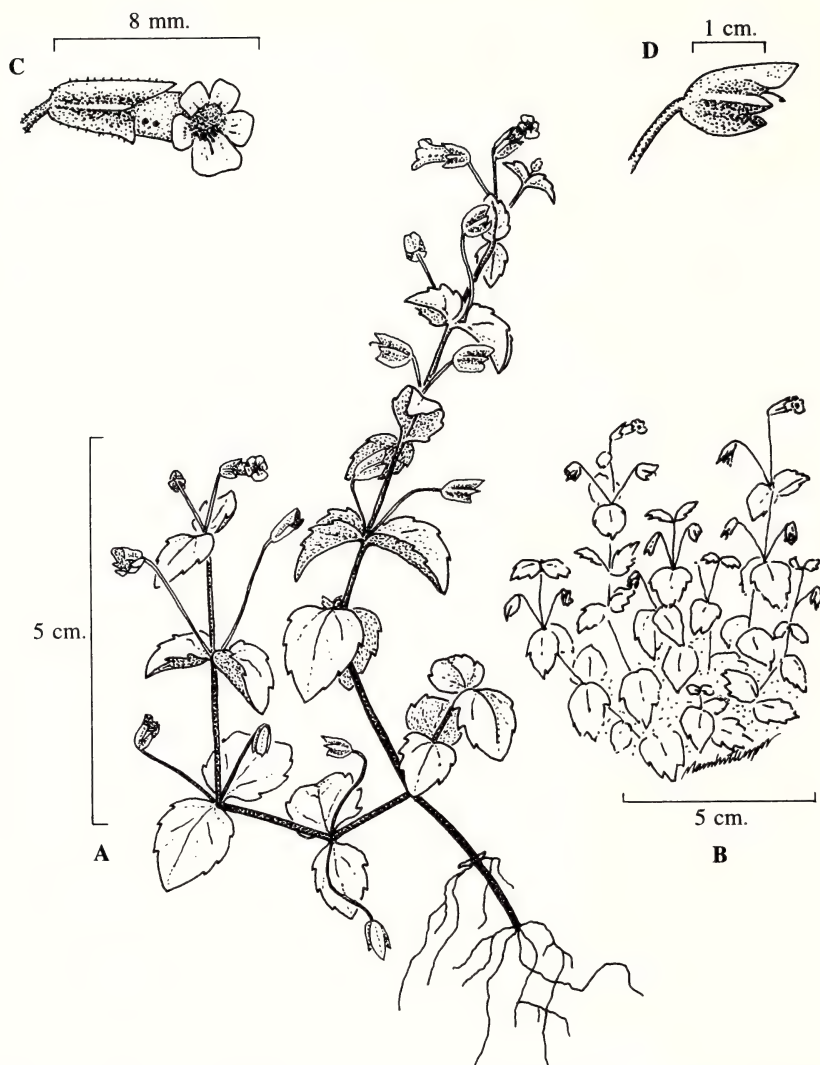


FIG. 2. *Mimulus minutiflorus* sp. nov. A. a branch drawn from a live plant grown from seeds of the type collection UT 119,045. B. habit, whole plant. C. flower. D. fruiting calyx.

chromosome number compared to *M. wiensii* warrants recognizing it as a new species, *M. yecorensis*, named for its region of occurrence.

The very small flowered populations crossed readily with each other (Table 3) but only formed one nearly sterile F_1 hybrid with one population of *M. wiensii*. They did not cross with *M. yecorensis*,

with which they might have been expected to hybridize on the basis of chromosome numbers (Table 3). Considering its genetic isolation, distinctive morphology, and tetraploid or higher chromosome numbers, I conclude that the very small flowered populations represent a second new species, *M. minutiflorus* named for its distinctive, tiny flowers.

Thus, the *M. wiensii* complex includes in addition to *M. wiensii*, 2 new species, *M. yecorensis* and *M. minutiflorus*.

THE NEW SPECIES

Mimulus yecorensis Vickery, sp. nov. (Fig. 1)—TYPE: MEXICO, Sonora, 17 km east of Yecora on México 16, on mossy banks of small stream, *Dan A. Polhemos s.n.*, 26 April 1982, *Vickery culture 13,257* (holotype: UT; isotypes: UC, DS, US, GH, RSA, MICH, SRSC, MEXU).

Plantae succulentae, humile repentes, tegetes densam formantes; caules virides, prostati ad libere nodos radicales, ramosissimi usque ad 60 cm longos; folia opposita, laeta, ovata ad orbicularia, 1–3 cm longa, 1–3 cm latis, serrulata, palmate 3–5 venis; flores stantes supra tegetes herbarum in gracilibus pedicellis 2.5–4.0 cm longis; calyx quinquelobus, campanulatus in maturitate obturbinescens, 5–9 mm longus; corolla bilabiata, 1.3–1.8 cm longa, 1.0–1.3 cm lata, flava, faux punctis ruberis; stylus 1; stigma bilabiatum, sensitivum; stamina 4, didynama, stylo breviores; capsula ovata; semina ellipsoidea, 0.3–0.4 mm longa, brunnea fusca; $n = 32$, *Mimulus wiensii* affilis.

Plants low, creeping, forming dense mats. Stems glabrous, green occasionally tinged with red towards apex, up to 60 cm or more in length, and much branched in pairs from nodes. Roots fibrous and slender. Leaves opposite, bright green above and below, ovate to orbicular, 1–3 cm long by 1–3 cm wide, serrulate, and palmately 3–5-veined. Petioles green, glabrous to pubescent along the margins, 1–4 cm long, diminishing in length towards apex. Flowers standing above mat of herbage. Pedicels slender, green occasionally tinged with red, approximately 0.5 mm in diameter, 2.5–4.0 cm long, longer than subtending leaf. Calyx 5-lobed, campanulate becoming obturbinate in maturity, 5–9 mm long, green to tinged with red at base, teeth triangular, upper longest, 2 lower curving inward in maturity. Corolla 5-lobed, 1.3–1.8 cm long, 1.0–1.3 cm wide, bilabiate, yellow, throat with red dots, lobes entire to slightly notched. Style 1, glabrous half again as long as calyx. Capsule ovate, less than half as long as calyx. Seeds ellipsoidal, 0.3–0.4 mm long, dark brown. $n = 32$.

Distribution. Known only from the Yecora area, Sonora, Mexico, where it grows on moist stream banks in the pine forest.

Mimulus minutiflorus Vickery, sp. nov. (Fig. 2)—TYPE: MEXICO, Durango, km 165.5 on México 40 in ephemerally moist, sunny areas in the pine forest. Elevation 2220 m. *R. K. Vickery Jr.* 2901, 12 May 1976, *culture number* 12218. (holotype: UT; isotypes: UC, DS, US, GH, RSA, MICH, SRSC, MEXU).

Herbae parvae, erectae and glabras; caules filo metalico similes, 5–20 cm alti, cum ramis ad nodos humiliores; folia opposita, ovata, 5–25 mm longa, 5–20 mm lata, serrulata, palmate 3–5 venis; flores in paribus axillaribus; pedicelli puberuli, 1–2 cm longi, virides, saepe rubrotincti; calyx quinquelobus, obturbatus, 5–6 mm longus in maturitate extendens ad 7–8 mm; corolla 5–6 mm longa, 5–8 mm lata, bilabiata, flava, punctis rubris in fauce; stylus 1; stigma bilabiatum, sensitivum; stamina 4, didynama, stylo breviores; capsula oblonga, semina ellipsoidea, 0.3–0.4 mm longa, fusca brunnea; $n = 32, 32\pm, 48\pm, 64\pm$; *Mimulus wiensii* affilis.

Plants small, 5–20 cm high, erect, ephemeral annuals. Stems slender, 1–2 mm in diameter, wiry, terete, green occasionally tinged with red, glabrous to puberulent, with opposite branches, rooting at lower nodes. Roots fibrous. Leaves opposite, ovate 5–25 mm long, 5–20 mm wide, serrate, palmately 3–5-veined, green above and below, glabrous at lower nodes to puberulent at upper nodes. Petioles glabrous, green, shorter than the leaves, 5–10 mm long at lower nodes diminishing upwards to 1 mm or less. Flowers in axillary pairs, rarely single. Pedicels puberulent, slender, 0.5 mm or less in diameter, 1–2 cm long, green occasionally tinged with red. Calyx 5-lobed, obturbinate, 5–6 mm long, lengthening to 7–8 mm in maturity, puberulent to nearly glabrous in maturity, green to tinged with red along the ridges, teeth triangular, upper tooth longest, the 2 lower curving inwards in maturity. Corolla 5-lobed, 5–9 mm long, 5–8 mm wide, bilabiate, yellow, throat with red dots, lobes entire. Style 1, glabrous, equaling longest calyx lobe in length. Capsule oblong, less than half length of calyx. Seeds ellipsoidal, 0.3–0.4 mm long, dark brown. $n = 32, 32\pm, 48\pm, 64\pm$.

Distribution. Near the crest of the Sierra Madre in the states of Durango and Sinaloa, Mexico, where it grows in sunny, ephemerally moist little swales.

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of the 2 new species. I thank the editor and 2 anonymous reviewers for their many insightful, helpful suggestions.

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NOTES

WING REDUCTION IN ISLAND *COREOPSIS GIGANTEA* ACHENES.—Paula M. Schiffman, Department of Biology and Center for the Study of Biodiversity, California State University, Northridge, CA 91330-8303.

Sherwin Carlquist (Quarterly Review of Biology 41:247–270, 1966; Evolution 20: 30–48, 1966; Brittonia 18:310–335, 1966) noted that island organisms often have reduced dispersibilities associated with reductions in wings or other dispersal structures. Among island plants, “precinctiveness” is common and an inability to disperse long distances is adaptive (Carlquist op. cit.). This is because the geographic extents of habitats of island species are often small and dispersal-enhancing morphologies increase probabilities of being transported beyond the bounds of these narrow habitats. In the most extreme cases, diaspores might be dispersed off an island and lost at sea (Eliasson, in Vitousek, Loope, and Adersen [eds.], Islands: biological diversity and ecosystem function, Springer-Verlag, NY, 1995; Cody and Overton, Journal of Ecology 84:53–61, 1996). Recently, Cody and Overton (op. cit.) documented rapid and significant reductions in pappus volume in *Lactuca muralis* and *Hypochaeris radicata* on some British Columbia islands. The strong selection for loss of dispersibility that they found suggested that similar selective forces should also be strong on other islands, resulting in widespread reductions in dispersibility among island species.

Such reductions should be apparent if the morphologies of diaspores of island plant species are compared to the morphologies of diaspores of their close mainland relatives. The following are the results of a small comparative study of achene morphologies of island and mainland populations of the perennial composite, *Coreopsis gigantea* (Kellogg) H. M. Hall. The specific question addressed was: when compared to achenes of a mainland population, do achenes of an island population exhibit morphologies consistent with a loss of dispersibility?

Achenes were haphazardly collected from a *C. gigantea* population on Bird Rock (a small islet located in the channel 0.4 km off-shore from the isthmus at Santa Catalina Island) and from a mainland population near Zuma Beach (Los Angeles Co.). Wing widths, seed widths, and achene lengths were measured to the nearest 0.01 mm using digital calipers (Fowler Ultra-Cal II; $n = 100$ achenes for each population). These island and mainland data were evaluated statistically using 2-sample t -tests ($\alpha = 0.05$; SYSTAT 5.2).

Small but highly statistically significant differences between the island and mainland populations were found for each of the achene characteristics examined (Fig. 1). The most striking difference was in wing width. Wings of achenes collected from the island (Bird Rock) population were, on average, 31.2% narrower than the wings of achenes from the mainland (Zuma Beach) population. In addition, seeds of Bird Rock achenes were 13.8% narrower and 18.8% longer than those from the mainland. It appears that the Bird Rock population may have experienced selection for reduced dispersibility similar to that observed by Cody and Overton (op. cit.). Moreover, this limited comparison suggests that *C. gigantea* achenes produced on California's Channel Islands have dramatically different morphologies than those produced by plants on the mainland.

These findings seem to support the Carlquist's hypothesis regarding precinctiveness in island plants and clearly merit further investigation. The 2 sites sampled for this study constituted only a very small subset of all island and mainland sites that support *C. gigantea*, a species that occurs along a narrow coastal strip from San Luis Obispo Co. through Los Angeles Co. (Sharsmith, Madroño 4:209–231, 1938; Smith, Sida

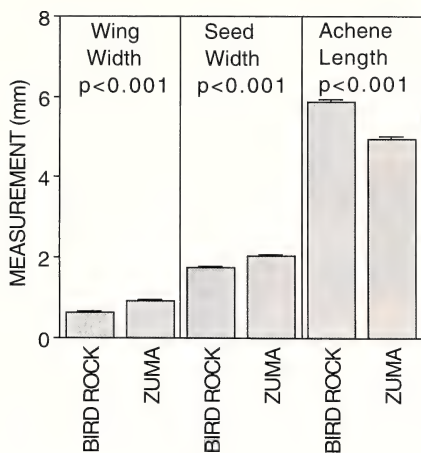


FIG. 1. Comparisons of mean (\pm SE) *Coreopsis gigantea* wing widths, seed widths and achene lengths for island (Bird Rock) and mainland (Zuma Beach) populations.

10:276–289, 1984) and on all of the Channel Islands (Junak et al., A flora of Santa Cruz Island, Santa Barbara Botanic Garden, 1995). In order to more fully understand these apparent differences in island and mainland achene morphologies and their relevance to dispersal and fitness, a more comprehensive and detailed examination of *C. gigantea* achenes (collected from several Channel Island and mainland locations) is currently underway.

I thank Roy van de Hoek for his assistance in the field and Sherwin Carlquist for his thoughtful review of an earlier version of this manuscript.

THE IDENTITY OF THE NAME *LUDWIGIA SCABRIUSCULA* KELLOGG.—Shirley Graham, Department of Biological Sciences, Kent State University, Kent, OH 44242 and David Keil, Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407.

The identity of the name *Ludwigia scabriuscula* Kellogg (Proc. Calif. Acad. Sci. 7:78. 1876) has apparently been somewhat a mystery since shortly after the species was described. No type material is known in BM, CAS, GH, UC, or US where Kellogg collections might be found and the description, although detailed, is problematic. It does not apply unambiguously to *Ludwigia* (Onagraceae) or any similar genus. Within four years of publication, the species was synonymized under *Ammannia latifolia* L. (Lythraceae) by Sereno Watson, who qualified his decision with the word “apparently” (Bot. Calif. 2:447. 1880). Mary Curran (Bull. Cal. Acad. Sci. 1:128–151. 1884) in reviewing the Kellogg species, accepted the synonymy without comment. It is possible that she did not see authentic material because the existence of some Kellogg types was already questionable at that time. Emil Koehne, monographer of *Ammannia*, saw no specimens of *Ludwigia scabriuscula*. He accepted Watson’s synonymy in “Lythraceae of the United States” (Bot. Gaz. 10:269. 1885) and later in his monograph of the Lythraceae (*Das Pflanzenreich* IV. 216:50. 1903).

Graham (J. Arnold Arbor. 66: 418. 1985) excluded *L. scabriuscula* from the synonymy of *A. latifolia* on morphological and geographical grounds. No *Ammannia* are known to have an inferior ovary (inferred by the generic assignment), scabrous

minutely-toothed leaves, long-clawed petals, or 4-lobed stigmas. The style, which is described as twice as long as the floral tube ("calyx"), is practically non-existent in *A. latifolia*, although it is long in some other species of *Ammannia*. Further, the presence of *A. latifolia* in California has never been verified. Its distribution is primarily circum-Caribbean with extensions northward along the Atlantic Coast and with a few disjunct sites in South America.

Several taxonomists including Bruce Bartholomew, Barbara Ertter, Peter Raven, and others with an extensive knowledge of the California flora, have considered with us whether any known genera match the Kellogg description. All agree that *Ammannia* remains the best choice. Features from the protologue of *L. scabriuscula* that match *Ammannia* are: stems slightly angled, leaves sessile, opposite, entire, oblong-linear, subcordate; flowers axillary, 6–9 whorled at a node, eight-angled with secondary teeth (in *Ammannia* these are the lobes of the epicalyx); and subquadrangular, ovoid capsules with reddish brown, obovate, minutely striated seeds. The habitat along muddy margins of streams and lakes is typical of *Ammannia*.

Two species of *Ammannia* occur in California. Both have long, slender styles. *Ammannia coccinea* Rottb. is an erect plant distinguished by 3–12-flowers per axil on distinct pedunculate cymes and deep rose-purple petals. *Ammannia robusta* is often decumbent with long basal branches, 1–3 sessile or subsessile flowers per axil, and pale lavender to nearly white petals. Watson would not have been familiar with *A. robusta* because, although it was present in California in the 1800s (e.g., Cache Creek, *Bolander in 1864* UC; Tulare Lake, 1877, *Lemmon 1402* GH; Los Angeles Co., 1889, *Hasse s.n.* CAS; Sacramento Co., 1893, *Jepson 14083* JEPS), it was not generally recognized as distinct from *A. coccinea* until 1985.

Morphological discrepancies in the description of *Ludwigia scabriuscula* with respect to *Ammannia* are judged to be erroneous observations. Scabulose, "obsoletely-toothed" leaves are probably the result of dessication which brings interior crystals into slight surface relief on herbarium specimens. The ovary was likely misinterpreted by Kellogg as inferior due to the closely investing, persistent floral tube. Of the two possible choices in *Ammannia*, *A. robusta* Heer & Regel (Index Sem. Horto Bot. Turic. adn. 1. 1842) most closely matches the description of *L. scabriuscula* by its basal branching, flowers few at the nodes, and pale petals. We therefore refer the name *Ludwigia scabriuscula* to the synonymy of *Ammannia robusta*. The nomenclature is not affected by this taxonomic decision because the name *A. robusta* predates the *Ludwigia* epithet.

NOTEWORTHY COLLECTIONS

ARIZONA

UTRICULARIA MINOR L. (LENTIBULARIACEAE).—Apache Co., Fort Apache Indian Reservation, N33°56'25", W109°50', elev. 2160 m, Lake Woolsey, 24 June 1996, Meyers-Rice s.n. (ARIZ 326165). Scattered specimens occur in the SW portion of this *Pinus ponderosa*-bordered shallow lake, especially on margins of floating mud flats in 1.5 m of water, 20 m from the shore. Associated with *Utricularia macrorhiza*, *Menyanthes trifoliata*, *Alisma triviale*, and *Sparganium*.

Previous knowledge. Circumboreal throughout Europe, Asia, and North America; in the USA extending south to California!, Nevada, Utah, Colorado, Nebraska, Iowa, Illinois, Indiana, Michigan, Pennsylvania, and New Jersey. Previously reported in Arizona but these records are incorrectly identified specimens of *Utricularia macrorhiza* LeConte (ARIZ!, ASC!, ASU!, DES!). Errors in identification are usually due to the plastic nature of *U. macrorhiza* which is particularly extreme when it is stressed; sterile specimens of the two species are easily distinguished by the presence of well-developed apical and lateral leaf setulae on *U. macrorhiza*, and the production of dimorphic shoots by *U. minor*—one type bearing leafy portions with bladders, the other type bearing only bladders more or less anchored in mud (P. Taylor, *The Genus Utricularia: a taxonomic monograph*, Royal Botanic Garden, Kew, 1989). These characters were subsequently reproduced by plants in cultivation.

Significance. This is the first correctly identified record for Arizona, and is a southern extension of the plant's range in North America. Previous searches of high elevation wetlands in Arizona have failed to detect it, although the closely related species *U. macrorhiza* is occasionally encountered in ponds at elevations greater than 2400 m. This record may represent a chance and ephemeral introduction by wildfowl. The station containing *U. minor* is interesting for its relatively low elevation as well as for the presence of *Menyanthes trifoliata*, which in Arizona is recorded in only one other location. Careful monitoring of the site during 1996 failed to reveal any flowers suggesting *U. minor* rarely flowers (or does not flower) in Arizona, and may reproduce by vegetative means only. *Utricularia macrorhiza* flowers regularly in this and other Arizona wetlands.

—BARRY A. MEYERS-RICE, P.O. Box 72741, Davis, CA 95617.

OREGON

LIGUSTRUM VULGARE L. (OLEACEAE).—Benton Co., Corvallis, Jackson-Frazier Wetland, in a wet wooded area with *Fraxinus*, *Rubus*, *Crataegus*, *Rosa*, *Alopecurus*, *Ranunculus*, T11S, R5W, DLC 45 or 46, elev. 69 m, 16 June 1996, *R. Halse* 5055 (OSC, duplicates to be distributed); same locality, in dry woods with *Acer*, *Rubus*, *Crataegus*, *Rosa*, *Cornus*, 4 July 1995, *R. Halse* 4937 (OSC, BH, SBBG).

Previous knowledge. This European native is a commonly cultivated ornamental. It has escaped in the northeastern USA (H. Gleason and A. Cronquist, *Manual of vascular plants of northeastern United States and adjacent Canada*, New York Botanical Garden, Bronx, 1995) and in Utah (S. Welsh et al., *A Utah flora*, Great Basin Naturalist Memoirs No. 9, 1987).

Significance. First report for Oregon.

EPILOBIUM HIRSUTUM L. (ONAGRACEAE).—Morrow Co., along U.S. Hwy 730, about

4 miles west of Umatilla, common in a wet roadside ditch with *Lythrum*, *Mimulus*, *Typha*, *Cirsium*, *Sonchus*, *Solidago*, T5N, R27E, S21, elev. 90 m, 6 July 1996, *R. Halse 5081* (OSC, MO, RSA, NY); Wasco Co., along Interstate Hwy 84 one mile W of its junction with Oregon Hwy 206 at Celilo Park, in wet area with *Melilotus*, *Asclepias*, *Cirsium*, *Sonchus*, *Rosa*, *Hypericum*, T2N, R15E, S20, elev. 69 m, 2 August 1996, *R. Halse 5145* (OSC, MO, UC, US).

Previous knowledge. This weedy Eurasian species is found in moist disturbed sites from southern Maine and Quebec to Maryland, west to northern Ohio, Michigan and northeast Illinois (Gleason and Cronquist op cit.). In Washington, it is known from wet places west of the Cascades as at Bellingham and Bingen (C. L. Hitchcock and A. Cronquist, *Flora of the Pacific Northwest*, Univ. of Washington Press, Seattle, 1973).

Significance. First record for Oregon.

—RICHARD R. HALSE, Department of Botany and Plant Pathology, 2082 Cordley, Oregon State University, Corvallis, OR 97331.

WASHINGTON

PITYOPUS CALIFORNICUS (Eastw.) H. F. Copel. (ERICACEAE).—Thurston Co., Fort Lewis Military Reservation, Rainier Training Area, 6.5 km NNE of the town of Rainier, WA, latitude 46°56'43"N, longitude 122°40'00"E, in 60-year-old *Pseudotsuga menziesii* stand, with *Gaultheria shallon*, *Pyrola* spp., and abundant moss (*Eurhynchium oreganum*), T17N R1E S22 NE¼ SW¼, 2 plants in deep moss, 130 m, 7 July 1995, *D. Thysell and S. Ball 735* (RSA, WTU) (verified by G. Wallace, RSA).

Previous knowledge. Known primarily from SW Oregon and N California. Though early collections are known from Humboldt Co., CA (V. Rattan 1878) and the Coast Range near Roseburg, OR (T. Howell 1887), the location of the northernmost known collection is from north of Mt. Hood, OR (*Pityopus oregona* Small, *Thomas Howell s.n.*, 3 July 1891, Holotype: NY). The Mt. Hood site has never been relocated. The subsequent northernmost collections are from the vicinity of Eugene, OR.

Significance. First record for Washington, a range extension of ca. 170 km north from the 1891 Howell collection locality and ca. 280 km north of other known sites in Oregon.

The field work leading to this report was supported by the U.S. Army, Ft. Lewis. We are grateful to Gary Wallace for confirmation of our identification and for providing records of other collections.

—DAVID THYSELL, ANDREW B. CAREY, and STACEY BALL, U.S. Forest Service, Pacific Northwest Research Station, Olympia Forestry Sciences Laboratory, 3625 93rd Ave. SW, Olympia, WA 98512.

CALIFORNIA

LARREA TRIDENTATA (DC.) Cov. (ZYGOPHYLLACEAE).—Kern Co.: Elk Hills, Naval Petroleum Reserve No. 1 (NPR-1), T31S, R24E, S2, 7 mature plants southeast of well 65-2G, 207 m, 24 June 1997, *J. M. Hinshaw s.n.* (UC); Kern Co.: Elk Hills, NPR-1, T31S, R24E, S4, 2 mature plants on W slope between wells 35-4G and 45-4G, 1020 ft (311 m), 24 June 1997, *J. M. Hinshaw s.n.* (UC); Kern Co.: Elk Hills, NPR-1, T31S, R23E, S10, 1 mature and 2 young plants 0.3 mi E of U.S. Navy Mercedes well, on S slope E of large wash, 281 m, 24 June 1997, *J. M. Hinshaw s.n.* (UC); Kern Co.: Elk Hills, NPR-1, T31S, R23E, S12, 1 mature plant 0.3 mi WNW of Gate 42 along Elk Hills Road, 244 m, 24 June 1997, *J. M. Hinshaw s.n.*

(UC); Kern Co.: Elk Hills, NPR-1, T30S, R23E, S33, 2 mature plants along road W of well 344-33R, 390 m, 24 June 1997, *J. M. Hinshaw s.n.* (UC). Biometrics and seed and biomass samples of the 15 plants observed were taken in July and August 1996. Ten, 4, and 1 plants were judged to be in high, moderate, and low vigor classes, respectively. The plant exhibiting low vigor was judged to be the youngest individual. Number of basal stems for the 15 plants averaged 6.67 (range = 1–18). Maximum basal diameters averaged 0.28 m (range = 0.01–0.65 m). Basal circumferences averaged 0.87 m (range = 0.02–1.70 m). Maximum foliar diameters averaged 4.07 m (range = 0.17–7.30 m). Foliar heights averaged 2.22 m (range = 0.11–3.34 m). The 2 young plants were growing within 5 m of an adult plant that had the highest basal circumference and maximum basal diameter, and the second highest number of basal stems of any adult plant observed. A fire killed both young plants and scorched the associated adult and 2 other adult plants in 1997.

Previous knowledge. Widespread in the southwestern United States and Mexico. Reported by D. M. Porter (Zygophyllaceae, pp. 1098–1099 in J. C. Hickman [ed.], *The Jepson manual: higher plants of California*, 1993) to occur as far west as parts of the South Coast, San Jacinto Mountain, and Tehachapi Mountain geographic areas. Twisselmann (Wasmann Journal of Biology 25:1–395, 1967) reported 3 plants growing west of the Sierra Nevada Range in Sand Canyon above Poso Creek and a single celebrated plant known as the “Dead Man’s Bush” growing on the Antelope Plains near Point of Rocks (Twisselmann 315, 1387) and mentioned the report of an isolated plant formerly growing on the Caliente Canyon flood plain. F. Tahbaz (personal communication) of the UC Herbarium located one 1898 collection (A. A. Still *s.n.*) from “Tulare plains, a solitary bush”, possibly the same individual Twisselmann referred to as the “Dead Man’s Bush”.

Significance. Westernmost occurrence of sexually reproductive individuals of and possibly the westernmost extant occurrence of this species. Twisselmann’s reported Point of Rocks individual is situated on gated private lands and its persistence has not been recently verified. Porter (1993) reports that clones of this species may live 10,000 years, longer than any other living plants known. Determining the age and genotype of *L. tridentata* at NPR-1 may provide insights about the history of this long-lived species and help ecologists better understand the regional paleoecology and paleoclimatic regimes. Evidence of historic surface disturbance at the first collection location noted here indicates possible introduction of this species to NPR-1 by human agency.

—JAY HINSHAW, U.S. Department of Energy, Elk Hills Oil Field, 1601 New Stine Road, Suite 240, Bakersfield, CA 93309.

CALIFORNIA

GLIDITSIA TRIACANTHOS L. (FABACEAE)—Sacramento Co., Cosumnes River Preserve, Galt, CA, N38°16′, W121°24′, 2 May 1997, *Randall and Meyers-Rice s.n.* (DAV 134241). Five young plants ranging from 2 to 15 dm tall were found growing in primary Valley oak riparian forest approximately 2.5 km southeast of the intersection of Desmond Road and Bruceville Road. This forest is dominated by mature *Quercus lobata*, *Populus fremontii*, *Fraxinus latifolia*, *Acer negundo* var. *californicum*, and *Salix goodingii*. *Vitis californica* vines climb into the overstory and prominent understory plants include *Rubus discolor*, *R. ursinus*, *Toxicodendron diversilobum*, *Oenothera sarmentosa*, and *Bidens vulgata*.

Previous knowledge. Native to the Mississippi Valley of the USA. Precise details of the original range of *G. triacanthos* are vague but it is believed to be within the area bounded by western Pennsylvania, extreme southern Michigan and southeastern Minnesota, southeastern South Dakota and central Nebraska, western Oklahoma,

northwestern and eastern Texas east to Alabama and northwestern Florida and north to eastern Tennessee and West Virginia (H. A. Gleason and A. Cronquist, *Manual of vascular plants of northeastern United States and adjacent Canada*, 1991; E. L. Little, Jr., *Checklist of native and naturalized trees of the United States (including Alaska)*, 1953). *G. triacanthos* is widely used horticulturally and has escaped from cultivation and become weedy east of the Appalachian Mountains from South Carolina to New England, north into southern Ontario, and west as far as western Kansas (Great Plains Flora Association, *Flora of the Great Plains*, 1986; E. L. Little, Jr., op. cit.). The species has also been reported as escaping from cultivation in the Buenos Aires Province of Argentina (A. L. Cabrera and E. M. Zardini, *Manual de la flora de los alrededores de Buenos Aires*, 1978), South Africa (M. J. Wells et al., *A catalogue of problem plants in Southern Africa*, 1986), New South Wales, Australia (N. C. W. Beadle et al., *Flora of the Sydney Region*, 1991), and Hungary (M. Rejmánek, personal communication). A thornless form (*G. triacanthos* f. *inermis* (Pursh) Schneid.) is occasionally encountered in natural populations and has been embraced by the nursery trade as an ornamental and shade tree; cultivated specimens are usually of this form. The saplings we found on the Cosumnes River Preserve did not have thorns and were probably of this variety.

Significance. First record in a California wildland. The closest reported occurrence of *G. triacanthos* outside of cultivation is in far western Kansas, approximately 1700 km distant (F. C. Gates, *Annotated list of the plants of Kansas*, 1940). Previous collections in California are limited to ones from a weedy lot in Orange Co. (F. M. Roberts, Jr., *A checklist of the vascular plants of Orange County, California*, 1989). Two saplings, also believed to be *G. triacanthos* f. *inermis*, were removed from the same area of the Cosumnes River Preserve in 1994–1995 and we believe that a yet-undiscovered parent plant may be growing nearby in the dense riparian forest. It is also possible that seed-pods from cultivated plants upstream were carried to the preserve during seasonal floods. This species has potential to become a troublesome weed in riparian forests of California's Central Valley, so we uprooted all the individuals we found and will search the area for a 'parent' plant and additional saplings periodically for the next several years.

—JOHN M. RANDALL and BARRY A. MEYERS-RICE, The Nature Conservancy, Wildland Weeds Management and Research, Department of Vegetable Crops and Weed Sciences, University of California, One Shields Avenue, Davis, CA 95616.

CALIFORNIA

MELISSA OFFICINALIS L. (LAMIACEAE). Inyo Co., Alabama Hills near Lone Pine. One site, May 10, 1993, T16S, R36E, SE¼, NE¼ S9, altitude 1150 m, near Los Angeles Aqueduct, *Yoder 6383* (DeDecker Herbarium, being transferred to RSA). (Determined by Mary DeDecker).

Previous knowledge. See Madroño 43(4):528.

Significance. First record for Inyo Co. and eastern Sierra.

—VINCENT YODER, 743 Windsor River Road, Windsor, CA 95492.

PRESIDENT'S REPORT FOR VOLUME 44

Welcome to the California Botanical Society's 1997–1998 program year. As incoming President, on behalf of the Council and entire Society, I want to thank Wayne Ferren for successfully completing three years of service as President of the Society. Other new and returning Council Members for this program year include First Vice-President, Susan D'Alcamo; Second Vice-President, Diane Ikeda; Treasurer, Mary Butterwick; Past Treasurer, Holly Forbes; Corresponding Secretary, Sue Bainbridge; Recording Secretary, Roxanne Bittman; Council Members Tony Morosco, Jim Shevock, and Margriet Wetherwax; Graduate Student Representative, Staci Markos; Madroño Editor, Elizabeth Painter; and Conservation Chair, Niall McCarten. A society run by volunteers is only as good as its volunteer leadership and these are great ones! The Society thanks each of you!

Susan D'Alcamo organized an excellent slate of eight speakers for the 1997–98 Lecture Series. The lectures are held in the Valley Life Sciences Building on the University of California, Berkeley, campus and have been very well attended by members as well as many non-members. The Council appreciates the help of Staci Markos in expanding the Society's publicity of each meeting and also for helping with room reservations and the reception. An informal reception follows each presentation which allows an opportunity to mingle with the speaker, other botanists, and guests. Refreshments are furnished by the Jepson and University Herbaria. All members are invited and encouraged to attend the talks and receptions. The original concept for the reception came from Brent Mishler. We thank him and the Jepson and University Herbaria for providing space for the Council meetings, lecture series, and reception.

Diane Ikeda spent many hours organizing this year's Annual Banquet which will be held on 21 February 1998, at the Alumni House on the campus of the University of California, Berkeley. Our guest speaker will be Dr. Robert Ornduff, who is speaking on "The Roots of the California Flora".

Graduate Student Meetings are sponsored by the California Botanical Society every other year. They were last held in Claremont in 1996. Graduate Student Meetings will be held this year at University of California, Berkeley, on 21 February 1998. Our Graduate Student Representative, Staci Markos, was responsible for making arrangements for the meetings as well as for preparing announcements. Other Council Members (Sue Bainbridge, Roxanne Bittman, Tony Morosco, and Margriet Wetherwax) assisted her. Many thanks to her and all others who have worked on this project, for a job well-done.

The Society purchased a laptop computer with modem in 1997 to assist in maintaining our membership roster. An accurate, updated, easy-to-use membership list was seen as crucial to assisting the Treasurer, Corresponding Secretary, and Editor. We encountered some problems implementing the new database in 1997, including a software bug, which resulted in errors to our membership list. Tony Morosco has temporarily taken responsibility for the new database, working with Mary Butterwick and Susan Bainbridge to fix problems associated with implementing the new program. We sincerely apologize to any members in good standing who were considered otherwise. Please let Mary know if there appears to be any problem with your membership status.

I wish to acknowledge the contributions Mary Butterwick has made during the transition from a cardfile to computer-based membership directory. As Corresponding Secretary, Susan Bainbridge has also been quite busy and very diligent in responding to requests for information from members and non-members. The Recording Secretary, Roxanne Bittman, has done an outstanding job of accurately recording the min-

utes as well as contributing to the Council meetings. The Society also appreciates the contributions of Editor Elizabeth Painter and Council Members Margriet Wetherwax, Tony Morosco, and Jim Shevock.

In response to a request from Brent Mishler, Tony Morosco volunteered to develop an Internet web page for the Society. We look forward to the availability of a web site as a means to increase communication and membership. The Council instituted two awards in 1997. An "Outstanding Service Award", for which any member is eligible, and a "Certificate of Appreciation" policy for Board Members, in recognition of their contributions to the organization. The ISBN and Library of Congress numbers were recently received for the "Eighty Year Index to Madroño". The Index will be available for purchase early in 1998.

Two of the benefits of membership in the California Botanical Society are receiving the quarterly journal *Madroño* and being able to publish in it. The cost of publishing *Madroño* remains the Society's greatest expense. Therefore, the Council decided that authors should be Society members throughout the publication process. Verifying membership requires monthly coordination among the Editor (Elizabeth Painter), Treasurer (Mary Butterwick), and Corresponding Secretary (Susan Bainbridge).

The Society is owed a considerable sum in unpaid *Madroño* page charges. To help recover these, the Council instituted a policy in early 1997 that precludes publication of manuscripts from authors who have outstanding page charges. The Council will continue to evaluate all procedures involved in producing a high quality journal. The Society appreciates the support and patience of the Council members as well as the membership while we work through these new procedures.

—R. JOHN LITTLE, Ph.D.

EDITOR'S REPORT FOR VOLUME 44

Since the previous editor's report [see Madroño 43(4)], the journal received 78 manuscripts for review, including articles, notes, and noteworthy collections.

The 80-year index to Madroño, which has been in production for some time, should become available soon. The California Botanical Society website (developed by Tony Morosco and hosted by the University and Jepson Herbaria) should also come on line soon, and will provide information concerning Madroño.

Beginning with Volume 45, Madroño should have a new size, a new format, and new cover art. I want to thank the members of the Madroño ad hoc committee (Tony Morosco, Margriet Wetherwax, Sue Bainbridge) and the artist (Linda Ann Vorobik) for their time and efforts.

I must thank those persons who have made my job as editor easier: Jon Keeley, who continues to serve as book review editor; Steve Timbrook, who again assembled the Index and Table of Contents for Volume 44; Margriet Wetherwax, Elizabeth Neese, and Dieter Wilken who served as Noteworthy Collections editors; the Santa Barbara Botanic Garden, which generously provided Madroño a courtesy mailing address and voice mail, the Garden's director Ed Schneider, and the Garden staff who patiently handled mail and queries; Annielaurie Seifert at Allen Press who was a pleasure to work with and who, together with the other people at Allen Press who have worked on Madroño this year, made the editor's job much easier; members of the CBS executive council; the reviewers upon whom Madroño depends for advice (their names appear on a separate page of this issue); and so many others, especially Sue Bainbridge, Tony Morosco, Bob Patterson, John Strother, Margriet Wetherwax, and Dieter Wilken, who were always available with help and advice.

I apologize to authors and members for all the inconveniences of the past year. It is with some regret that I turn the editorship over to Kristina Schierenbeck. However, I know that it will be in more capable hands. I look forward to jointly compiling the first issues of Volume 45.

—ELIZABETH L. PAINTER

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INDEX TO VOLUME 44

Classified entries: major subjects, key words, and results; botanical names (new names are in **boldface**); geographical areas; reviews, commentaries. Incidental references to taxa (including most lists and tables) are not indexed separately. Species appearing in Noteworthy Collections are indexed under name, family, and state or country. Authors and titles are listed alphabetically by author in the Table of Contents to the volume.

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